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Revision of Australian *Eptesicus* (Microchiroptera: Vespertilionidae)

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Abstract

A classical morphological approach has been used to clarify the taxonomy of Australian *Eptesicus*. Multivariate analyses of 37 morphological measurements were undertaken to determine the phenetic relationships between the nine species recognised in this study: *E. pumilus* (Gray, 1841); *E. caurinus* Thomas, 1914; *E. douglasorum* Kitchener, 1976; *E. finlaysoni* sp. nov.; *E. darlingtoni* Allen, 1933; *E. troughtoni* sp. nov.; *E. regulus* (Thomas, 1906); *E. vulturnus* Thomas, 1914 and *E. baverstocki* sp. nov.

In Australian *Eptesicus* there are two broad phenetic groups. The first includes those species with a northern or inland distribution; the second those with a southern or inland distribution.

Introduction

Miller (1907) details the nomenclatural history of the genus *Eptesicus* [type species of *E. melanops* Rafinesque, 1820 (= *Vespertilio fuscus* Beauvois, 1796)] of North America. Since recognition of this genus, 35 species have been recognised by Corbet and Hill (1986), including species from Europe, Africa, Australia and South Amcrica. These additions have resulted in a widening of the initial generic concept of *Eptesicus* such that, apart from the similar dental formula, many species have little in common with *E. melanops* Rafinesque.

The external morphology and skull of certain species groups of *Eptesicus* are very similar to certain species of *Pipistrellus* Kaup, 1929 (and *Vespertilio* Linnaeus, 1758) save for the usual absence of thc anterior upper premolar of *Pipistrellus*. As occasional *Eptesicus* specimens do havc this additional premolar, its presence or absence is a dubious character on which to base a generic distinction (Tate 1942, Ellerman and Morrison-Scott 1951, Hill and Topal 1974, Kock 1969 and Heller and Volleth 1984). Ellerman and Morrison-Scott (1951) conclude that *Pipistrellus* is no more than a subgenus of *Eptesicus*, which itself might be referred to *Vespertilio*. Heller and Volleth (1984) suggest a de-emphasis of the importancc of the presence or absencc of this anterior premolar to distinguish *Eptesicus* and *Pipistrellus* because 'a multiply independent loss of the second premolar is easily

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imaginable'. They consider *Eptesicus* to be distinguishable from *Pipistrellus* (and *Vespertilio*) by the possession of 50 chromosomes (with a fundamental number of 48), a baculum that is relatively small and not stick-like and the presence of one or two pairs of upper premolars. On this basis Heller and Volleth (1984) consider the Australian species usually placed in *Eptesicus* belong to *Pipistrellus,* which they characterise as having a diploid chromosome number of 44 or less, a more or less stick-like baculum and one or two pairs of upper premolars. This view is somewhat appealing as the inclusion of the Australian species in *Eptesicus* results in a genus which has a peculiarly disjunct Oriental and Australian distribution, with no *Eptesicus* between southern Thailand *(E. demissus)* and Australia (see Koopman 1984). However, we recognise consistent differences between Australian *Eptesicus* and Australo-Papuan pipistrelles in the shape of the posterior palate and internal narial regions, the upper incisors and the morphology of the bacula and glans penis. As a consequence we are reluctant to consider these forms congeneric.

Troughton (1944*a*) proposed the generic name *Vespadelus* for the Australian species *Scotophilus pumilus* (= *Eptesicus pumilus*). This name was introduced without an accompanying diagnosis by Iredale and Troughton (1934). Troughton (1944*b*) proposed *Registrellus* for the composite specimen *Pipistrellus regulus* (= *Eptesicus regulus,* see Hill 1966) from southwestern Australia. Both *Vespadelus* and *Registrellus* are available names for a genus comprising the Australian forms currently placed in *Eptesicus,* but without a comprehensive phylogenetic appraisal of related Vespertilionidae, which is outside the scope of this study, we are unable to appraise the generic separability of the Australian species of *'Eptesicus'.*

The following eight forms of Australian *Eptesicus* have been recognised: *Eptesicus pumilus* (Gray, 1841); *E. pygmaeus* (Becker, 1858); *E. darlingtoni* Allen, 1933; *E. pumilus caurinus* Thomas, 1914; *E. pumilus vulturnus* Thomas, 1914; *E. regulus* (Thomas, 1906); *E. douglasorum* Kitchener, 1976 and *E. sagittula* McKean, Richards and Price, 1978. Until the mid 1970s workers [e.g. Tate (1942), Ride (1970)] considered all the described forms as subspecies of *Eptesicus pumilus.* Kitchener and Halse (1978) applied the available name *regulus* to the southwestern *Eptesicus,* a view supported by McKean *et al.* (1978) who also recognised *E. vulturnus.* At the time of this study the following five Australian *Eptesicus* species were generally recognised (e.g. McKean *et al.* 1978; Campbell and Kitchener 1980; Carpenter *et al.* 1978; Tidemann *et al.* 1981; Green and Rainbird 1984; Strahan 1984): *pumilus, regulus, vulturnus, douglasorum* and *sagittula. E. pygmaeus* (Becker, 1858; not Leach, 1825) was synonymised with *E. vulturnus* by McKean *et al.* (1978). Recent collections of Australian *Eptesicus* have revealed undescribed forms, necessitating this taxonomic revision. While we have applied classical morphological as well as modern numeric taxonomic techniques to identify species in this study, we acknowledge the co-operation of our colleagues at the South Australian Museum who have conducted a parallel electrophoretic study of Australian *Eptesicus.*

Methods

Morphology

Teeth – terminology of tooth structure follows Slaughter (1970) and is illustrated for upper and lower molars in Kitchener and Caputi (1985).

Measurements

Skull, dentary and externals – twenty seven measurements (in mm) of the skull and 12 external measurements were recorded from adult specimens only (listed in the sections 'Specimens Examined'). Measurements of holotypes or lectotypes or paratypes are listed in Appendix I. Subadults and juveniles were diagnosed on the basis of epiphyseal swellings of the metacarpal joints. The terminology used follows Kitchener and Caputi (1985). Colours of pelage and skin are capitalised where they follow the Ridgway (1912) colour charts.

All measurements were made with dial calipers. The positions of these measurements are indicated in Figure 1.

Coded characters and descriptive terms

The following coded characters were used in the phenetic analysis and where appropriate in the diagnoses and descriptions.

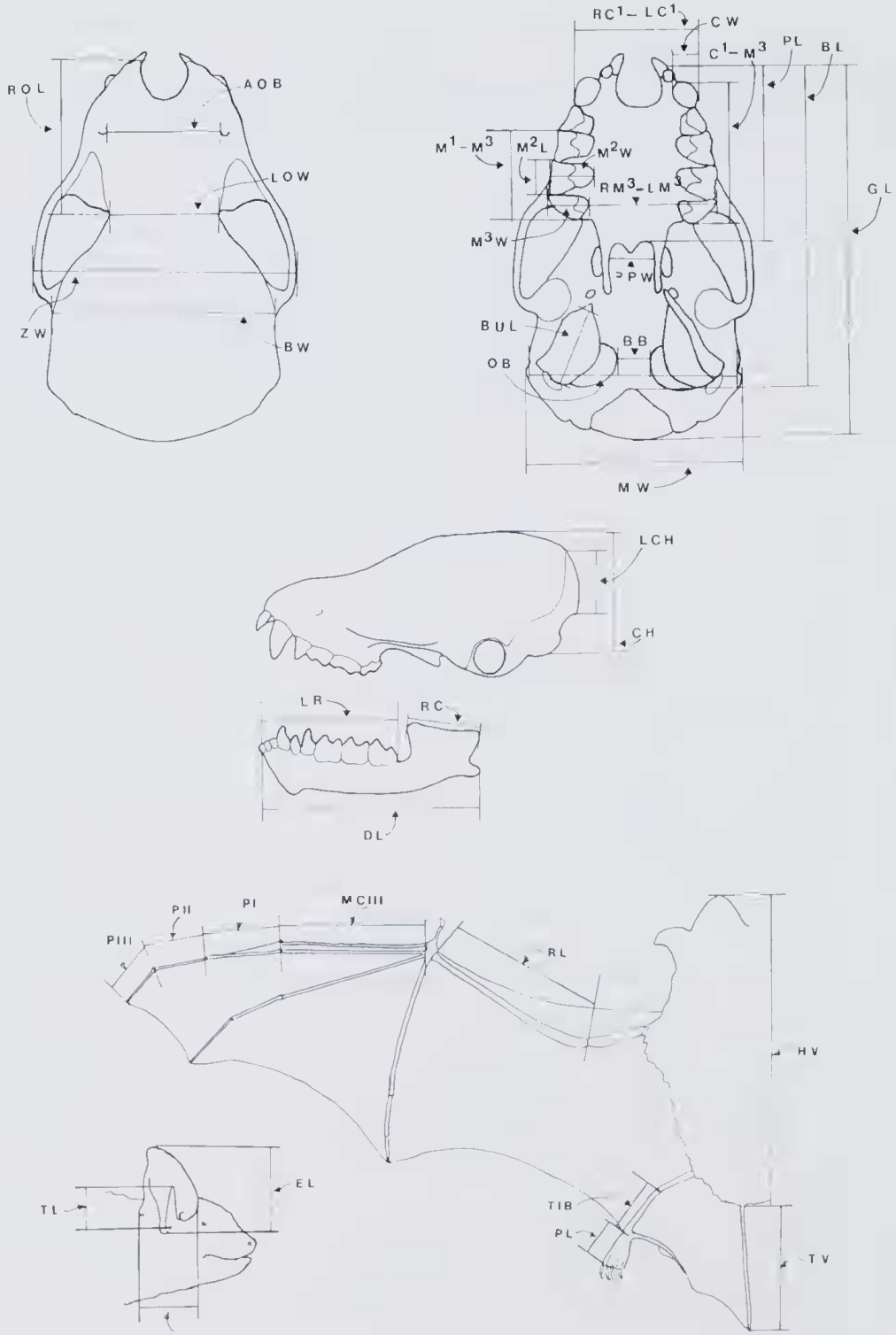
1. Anterior palatal emargination
   (o) - maximum width sited in the posterior one-third of emargination
   (i) - maximum width sited in the central one-third of emargination

2. Anterior palatal emargination
   (o) - wider than long
   (i) - maximum width equals length ("square")
   (ii) - longer than wide

3. Anterior palatal emargination (Figure 2*a*)
   (o) - shallow: does not extend beyond posterior margin of canine
   (i) - deep: terminates posterior to posterior margin of canine

4. Anterior narial emargination (Figure 2*b*)
   (o) - deep: extends to, or almost to, a line joining anterior margins of anteorbital foramina
   (i) - shallow: terminates well anterior to the above line

5. Relationship between basolateral pterygoid wing and foramen rotundum (Figure 2*c*)
   (o) - absent: wing absent or not extending to edge of foramen rotundum
   (i) - present: wing covers $<1/3$ of foramen rotundum
   (ii) - present: wing covers $>1/3 <2/3$ of foramen rotundum
   (iii) - present: wing covers $>2/3$ foramen rotundum


ROL
AOB
LOW
ZW
BW
RC1– LC1
CW
C1– M3
PL
BL
M1 – M3
M2L
M2W
RM3– LM3
GL
M3W
PW
BUL
BB
OB
MW
LCH
CH
LR
RC
DL
PIII
PII
PI
MCIII
RL
HV
TL
EL
EW
TIB
PL
TV

6. Dorsal inflation of cranium (Figure 2*d*)
   (o) - absent
   (i) - slight
   (ii) - moderate
   (iii) - pronounced

7. Crista M^1 and/or M^2 (Figure 3)
   (o) - absent LM^{1-2} and/or RM^{1-2}
   (i) - slight LM^{1-2} and/or RM^{1-2}
   (ii) - moderate LM^{1-2} and RM^{1-2}
   (iii) - large LM^{1-2} and RM^{1-2}

8. P^2
   (o) - present
   (i) - absent

9. I^2
   (o) - present
   (i) - absent

◀ Figure 1 Skull, dentary and external body measurements referred to in text and their recording points. GL: greatest skull length; AOB: anteorbital width, between anteorbital foramina; LOW: least interorbital width; LW: lacrymal width; ZW: zygomatic width; ROL: rostrum length, from LOW to anterior edge of premaxilla; MW: mastoid width, between mastoid processes; BW: braincase width, at centre of zygomatic-squamosal contact; CH: cranial height, lower arm of calipers placed level with pre- and basi-sphenoid, upper arm in contact with apex of skull; LCH: lambdoidal crest height; PL: palatal length, excluding postpalatal spine; PPW: postpalatal width; BL: basicranial length, between anterior edge of foramen magnum and anterior edge of premaxilla; BUL: bulla length, excluding eustachian part; BB: width of basi-sphenoid between cochlea; OB: distance outside bullae, caliper points in contact with antero-dorsal edge of tympanic ring; CW: canine width, maximum diameter at base; RC^1-LC^1: inter upper canine distance, at base of cusp; C^1-M^3: upper maxillary tooth row crown length, anterior edge of C^1 to posterior edge M^3; M^{1-3}: upper molar crown length, anterior edge M^1 parastyle to posterior edge M^3; M^2L: upper second molar crown length, anterior edge of parastyle to posterior edge of metastyle; M^2W: upper second molar crown width, lingual base of protocone to buccal face of paracone, at right angles to occlusal surface; M^3W; upper third molar crown width, as for M^2W; RM^3-LM^3 inter upper third molar distance, across buccal face of paracone to RM^3 and LM^3; LR: lower tooth row length, posterior edge M_3 to anterior edge of dentary; RC: angular ramus to dentary condyle, blade of caliper along anterior face of ramus and measuring to posterior edge of articular condyle; DL: dentary length, from condyle to anterior tip of dentary; HV: body length, tip of rhinarium to anus; TV: tail length, tip to anus; EL: ear length, apex to basal notch; EW: ear width across basal lobes; TL: tragus length; RL: radius length; MCIII: metacarpal III length; PI: digit III, phalanx I length; PII: digit III, phalanx II length; PIII: digit III, phalanx III length; TIB: tibia length and PL: pes length.

Table 1a, b Measurements in mm (see Figure 1 for code to characters) for adults of the nine species of *Eptesicus*. N, sample size; $\bar{X}$, mean; SD, standard deviation; Mn, minimum and Mx, maximum, (a) skull, dentary and teeth and (b) externals.

Table 1a

Species		Skull, Dentary and Teeth Characters																											
		GL	AOB	LOW	LW	ROL	ZW	MW	BW	CH	LCH	PL	BL	PPW	BUL	BB	OB	CW	RC-LC	C-M	M-M	MPL	MPW	MFW	LM	LR	DL	RC
E. pumilus	N	25	26	26	26	26	21	25	25	25	23	26	25	25	25	25	25	26	26	26	26	26	26	26	26	26	26	26	26
	$\bar{X}$	12.1	3.8	3.6	5.0	5.2	8.0	6.9	6.3	1.6	2.1	5.6	10.1	1.7	2.7	1.2	6.5	0.7	3.7	1.3	2.8	1.1	1.2	1.2	5.1	5.3	8.6	2.5	
	SD	0.27	0.14	0.15	0.17	0.19	0.21	0.22	0.14	0.11	0.22	0.17	0.21	0.19	0.12	0.08	0.18	0.06	0.15	0.09	0.05	0.05	0.05	0.04	0.11	0.13	0.20	0.10	
	Mn	11.3	3.5	3.2	4.5	4.8	7.6	6.3	6.0	1.1	1.8	5.1	9.8	1.2	2.5	1.1	6.1	0.6	3.1	1.1	2.7	1.0	1.1	1.2	4.8	5.0	8.1	2.3	
	Mx	12.7	4.1	3.9	5.2	5.5	8.1	7.2	6.5	1.8	2.6	5.9	10.5	2.0	3.0	1.3	6.8	0.9	4.0	1.6	3.0	1.2	1.3	1.3	5.2	5.5	8.8	2.6	
E. caurinus	N	11	12	12	11	12	25	10	11	10	10	37	11	11	12	10	10	12	12	12	12	12	12	12	12	11	11	11	
	$\bar{X}$	11.2	3.8	3.3	4.8	4.5	7.5	6.5	5.8	1.1	1.9	5.1	9.1	1.1	2.6	1.0	6.0	0.67	3.6	3.9	2.6	1.0	1.2	1.1	4.8	4.8	7.9	2.3	
	SD	0.31	0.16	0.11	0.19	0.20	0.23	0.20	0.17	0.19	0.21	0.19	0.27	0.12	0.10	0.14	0.18	0.06	0.12	0.15	0.11	0.07	0.07	0.08	0.16	0.16	0.25	0.09	
	Mn	10.6	3.6	3.0	4.3	4.1	7.1	6.2	5.5	1.0	1.2	4.8	8.9	1.2	2.4	0.7	5.6	0.6	3.1	3.6	2.5	0.9	1.0	1.0	4.5	4.5	7.4	2.1	
	Mx	12.0	4.2	3.5	5.3	5.0	7.9	7.0	6.2	1.8	2.3	5.6	10.0	1.7	2.9	1.3	6.5	0.8	3.8	4.2	2.9	1.1	1.3	1.3	5.2	5.1	8.6	2.5	
E. douglasorum	N	12	13	13	13	13	10	12	13	12	12	12	12	13	11	13	13	13	13	13	13	13	13	13	13	13	13	13	
	$\bar{X}$	12.8	4.1	3.5	5.5	5.3	8.1	7.2	6.3	1.9	2.2	5.9	10.9	1.6	2.8	1.1	6.6	0.8	4.2	1.7	3.1	1.2	1.3	1.3	5.5	5.7	9.2	2.7	
	SD	0.25	0.14	0.10	0.18	0.18	0.25	0.17	0.20	0.13	0.15	0.19	0.24	0.11	0.11	0.11	0.13	0.01	0.13	0.13	0.08	0.08	0.03	0.07	0.13	0.14	0.21	0.09	
	Mn	12.3	4.2	3.3	5.3	5.1	8.1	6.8	6.0	1.7	2.0	5.7	10.6	1.4	2.6	0.9	6.1	0.8	4.0	4.5	2.9	1.0	1.3	1.2	5.3	5.5	9.0	2.6	
	Mx	13.2	4.6	3.6	6.0	5.6	8.8	7.1	6.7	5.2	2.6	6.3	11.1	1.8	3.0	1.2	6.8	0.9	4.4	5.0	3.2	1.3	1.1	1.5	5.8	6.0	9.6	2.9	
E. finlaysoni	N	89	88	89	88	89	72	86	89	89	86	87	88	87	89	89	88	89	89	89	89	89	89	89	89	89	89	89	
	$\bar{X}$	12.4	4.1	3.4	5.4	5.0	8.3	7.1	6.2	4.7	2.1	5.6	10.5	1.6	2.8	1.1	6.5	0.8	4.0	4.4	3.0	1.1	1.3	1.3	5.3	5.3	8.8	2.6	
	SD	0.19	0.23	0.16	0.26	0.29	0.37	0.28	0.26	0.19	0.16	0.32	0.56	0.12	0.13	0.12	0.23	0.08	0.23	0.23	0.16	0.07	0.09	0.08	0.25	0.26	0.43	0.16	
	Mn	11.3	3.6	3.0	4.8	4.3	7.5	6.4	5.6	1.2	1.7	5.0	9.6	1.4	2.6	0.8	5.9	0.7	3.5	4.1	2.6	1.0	1.1	1.1	4.8	4.8	8.0	2.3	
	Mx	13.5	4.6	3.9	5.9	5.8	9.2	8.1	7.0	5.2	2.4	6.1	11.7	1.8	3.1	1.3	7.3	1.0	4.5	5.0	3.1	1.3	1.5	1.5	6.0	6.0	9.8	3.1	

Table 1a (continued)

Species		Skull, Dentary and Teeth Characters																										
		GL	AOB	LOW	LW	ROL	ZW	MW	BW	CH	LCH	PL	BL	PPW	BUL	BB	OB	CW	RC¹-LC¹	C¹-M³	M¹-M³	M²L	M²W	M³W	LM³	LR	DL	RC
E. darlingtoni	N	34	34	34	34	34	26	34	34	34	34	34	34	34	34	34	34	34	34	34	34	34	34	34	34	34	34	34
	X	13.4	4.1	4.0	5.5	5.7	8.7	7.6	6.8	5.0	2.3	6.1	11.4	1.9	3.0	1.3	7.1	0.8	4.2	4.9	3.3	1.2	1.4	1.4	5.7	5.9	9.6	2.7
	SD	0.34	0.16	0.09	0.19	0.26	0.28	0.24	0.19	0.11	0.18	0.22	0.37	0.14	0.15	0.15	0.23	0.07	0.15	0.18	0.13	0.07	0.08	0.11	0.21	0.22	0.30	0.11
	Mn	12.7	3.8	3.8	5.1	5.2	8.2	7.1	6.5	4.7	2.0	5.7	10.5	1.6	2.7	1.0	6.7	0.7	3.9	4.4	3.0	1.1	1.2	1.2	5.2	5.4	8.8	2.5
	Mx	14.1	4.5	4.1	5.9	6.2	9.3	8.0	7.2	5.2	2.8	6.5	12.0	2.3	3.3	1.6	7.6	0.9	4.4	5.2	3.6	1.3	1.5	1.6	6.1	6.3	10.1	3.0
E. troughtoni	N	24	25	25	25	24	14	25	25	25	23	24	24	25	25	25	24	25	25	25	25	25	25	25	25	25	25	25
	X	12.7	4.3	3.8	5.6	5.3	8.5	7.4	6.5	4.8	2.3	5.9	10.8	1.7	2.9	1.2	6.7	0.8	4.1	4.7	3.1	1.2	1.3	1.3	5.7	5.7	9.2	2.6
	SD	0.21	0.13	0.09	0.10	0.15	0.18	0.13	0.15	0.11	0.22	0.17	0.20	0.12	0.10	0.17	0.15	0.05	0.09	0.10	0.08	0.06	0.07	0.06	0.14	0.12	0.18	0.06
	Mn	12.2	4.1	3.6	5.3	4.9	8.2	7.2	6.2	4.6	1.7	5.6	10.3	1.5	2.7	1.0	6.5	0.7	4.0	4.5	2.9	1.0	1.2	1.2	5.4	5.5	8.8	2.5
	Mx	13.2	4.6	3.9	5.8	5.6	8.7	7.7	6.7	5.0	2.8	6.2	11.2	2.0	3.0	1.8	7.0	0.9	4.3	4.8	3.2	1.3	1.5	1.4	5.9	6.0	9.5	2.7
E. regulus	N	84	84	84	84	84	61	83	83	84	83	82	81	83	83	84	84	84	83	84	84	84	84	84	84	83	83	84
	X	12.7	4.1	3.5	5.3	5.4	8.3	7.3	6.4	4.4	2.2	5.8	10.8	1.6	2.8	1.3	6.7	0.8	4.0	4.5	3.0	1.1	1.3	1.2	5.2	5.6	9.1	2.6
	SD	0.30	0.17	0.18	0.20	0.22	0.27	0.21	0.24	0.20	0.21	0.21	0.30	0.12	0.11	0.14	0.19	0.08	0.19	0.16	0.11	0.07	0.08	0.08	0.21	0.18	0.28	0.13
	Mn	11.9	3.8	3.1	4.6	4.7	7.6	6.9	5.8	4.0	1.9	5.3	9.9	1.3	2.6	1.0	6.2	0.6	3.5	4.1	2.7	1.0	1.1	1.0	4.3	5.1	8.4	2.3
	Mx	13.4	4.6	4.0	5.7	5.8	8.9	8.0	6.9	4.9	2.9	6.4	11.5	1.9	3.0	1.6	7.2	1.0	4.5	4.8	3.3	1.4	1.5	1.4	5.6	5.9	9.7	2.9
E. vulturnus	N	34	34	34	34	34	31	34	34	34	34	34	34	34	34	34	34	34	34	34	34	34	34	34	34	34	34	34
	X	12.2	3.8	3.4	5.0	5.1	7.8	6.9	6.1	4.2	2.1	5.5	10.3	1.6	2.8	1.1	6.4	0.7	3.8	4.3	2.9	1.1	1.2	1.2	5.1	5.3	8.7	2.5
	SD	0.24	0.15	0.11	0.14	0.17	0.19	0.17	0.19	0.10	0.13	0.15	0.23	0.08	0.09	0.13	0.13	0.05	0.13	0.11	0.11	0.05	0.06	0.07	0.16	0.15	0.23	0.10
	Mn	11.8	3.5	3.2	4.8	4.7	7.3	6.6	5.9	4.0	1.9	5.2	9.8	1.5	2.6	0.8	6.2	0.7	3.6	4.1	2.5	1.0	1.1	1.1	4.8	5.1	8.3	2.3
	Mx	12.7	4.1	3.6	5.4	5.4	8.3	7.3	6.8	4.4	2.5	5.8	10.7	1.8	3.0	1.4	6.7	0.9	4.1	4.6	3.1	1.2	1.4	1.4	5.4	5.8	9.2	2.7
E. baverstocki	N	25	25	25	25	25	18	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25	25
	X	12.1	3.8	3.2	5.0	5.0	7.9	6.9	6.0	4.1	1.9	5.4	10.3	1.4	2.8	1.2	6.3	0.7	3.8	4.2	2.9	1.1	1.3	1.2	5.0	5.1	8.6	2.5
	SD	0.27	0.16	0.08	0.21	0.14	0.25	0.19	0.16	0.14	0.13	0.17	0.25	0.10	0.10	0.15	0.17	0.05	0.19	0.14	0.10	0.07	0.09	0.09	0.16	0.20	0.29	0.11
	Mn	11.6	3.5	3.0	4.6	4.8	7.6	6.4	5.6	3.9	1.6	5.1	9.8	1.2	2.5	0.8	6.0	0.6	3.5	3.9	2.7	0.9	1.1	1.1	4.7	4.7	8.1	2.3
	Mx	12.5	4.2	3.3	5.5	5.3	8.4	7.2	6.3	4.4	2.1	5.7	10.6	1.6	2.9	1.5	6.6	0.8	4.2	4.5	3.0	1.2	1.4	1.4	5.4	5.5	9.2	2.7

Table 1b

Species		External Characters											
		HV	TV	EL	EW	TL	RL	MCHL	PL	PH	PHL	FIB	PL
E. pumilus	N	24	24	25	24	25	25	25	25	25	24	25	25
	X	39.4	30.7	10.5	8.0	5.3	30.6	29.4	11.5	8.9	7.7	12.6	5.2
	SD	2.32	1.43	0.70	0.44	0.52	1.14	1.21	0.49	0.51	0.47	0.53	0.18
	Mn	35.0	27.6	9.0	7.0	4.6	28.1	27.3	10.5	7.6	6.6	11.6	4.2
	Mx	44.2	33.7	11.9	8.8	6.5	32.9	32.2	12.4	9.8	8.6	13.8	6.4
E. caurinus	N	36	39	38	37	37	39	39	39	39	39	39	38
	X	36.7	30.2	10.1	7.3	5.3	29.5	28.6	10.6	10.1	5.5	11.4	4.3
	SD	2.06	2.01	0.87	0.49	0.61	1.08	1.21	0.51	0.72	0.50	0.48	0.39
	Mn	32.1	24.1	8.3	6.5	3.8	26.6	25.9	9.8	7.9	4.4	10.7	3.6
	Mx	40.0	34.8	12.3	8.3	6.5	31.7	31.9	12.0	12.1	6.8	12.4	5.5
E. douglasorum	N	13	8	13	13	13	11	13	13	13	12	10	10
	X	39.7	36.3	11.9	8.6	5.3	36.2	35.0	11.1	11.5	6.1	14.3	5.2
	SD	2.13	1.02	0.38	0.28	0.48	1.14	1.36	0.48	0.41	0.49	0.61	0.35
	Mn	35.3	35.2	11.3	8.1	4.9	34.3	32.7	10.0	10.8	5.3	13.6	4.8
	Mx	43.5	37.9	12.5	9.0	6.6	37.6	37.0	11.7	12.2	7.0	15.5	6.1
E. finlaysoni	N	83	79	84	84	84	84	84	84	83	82	82	82
	X	40.1	35.2	11.1	8.2	5.5	32.8	32.3	12.3	11.2	6.7	13.6	4.9
	SD	2.51	2.93	0.73	0.42	0.56	1.18	1.60	0.65	0.82	0.61	1.00	0.39
	Mn	34.3	30.7	9.3	6.9	4.1	29.8	29.3	11.0	9.2	5.0	11.4	4.0
	Mx	46.4	42.0	13.2	9.5	6.9	36.7	36.1	13.8	13.0	7.9	16.2	6.0
E. darlingtoni	N	30	29	31	31	31	32	33	33	33	31	31	30
	X	44.1	33.5	11.8	8.9	6.5	34.6	32.9	13.0	9.6	8.8	13.7	5.9
	SD	3.08	2.08	0.82	0.42	0.70	1.44	1.05	0.60	0.56	0.68	0.52	0.39
	Mn	38.4	29.2	10.1	7.9	4.9	32.5	30.9	11.8	8.7	7.6	12.3	5.2
	Mx	48.9	38.0	13.1	9.8	7.7	37.2	35.1	14.2	10.8	10.0	14.4	7.0
E. troughtoni	N	17	16	17	17	17	17	17	17	17	17	17	17
	X	41.5	35.3	11.4	8.4	5.6	34.8	34.0	12.6	11.0	7.1	13.6	5.4
	SD	1.71	2.25	0.66	0.38	0.73	0.89	0.72	0.54	0.73	0.59	0.42	0.37
	Mn	37.5	31.4	10.1	7.6	4.6	33.0	32.6	11.5	9.3	6.5	12.7	4.8
	Mx	44.2	37.9	12.5	9.2	7.4	36.4	35.1	13.5	12.6	8.3	14.2	6.2
E. regulus	N	75	72	77	76	77	77	77	77	77	75	77	76
	X	41.4	31.7	11.1	8.6	5.9	31.2	30.2	11.2	9.0	7.2	12.7	5.4
	SD	2.47	1.80	0.70	0.48	0.48	1.49	1.24	0.54	0.57	0.56	0.56	0.46
	Mn	36.2	28.5	9.0	7.4	4.4	28.0	27.0	9.8	7.5	6.0	11.4	4.3
	Mx	46.6	39.0	12.9	9.6	7.1	34.4	32.7	12.4	10.3	9.0	13.9	6.7
E. vulturnus	N	33	32	34	33	31	34	34	34	34	22	22	22
	X	40.2	30.9	10.6	8.4	5.5	28.4	27.6	11.5	8.9	6.7	11.8	5.0
	SD	2.71	1.86	0.72	0.45	0.45	1.20	1.42	0.48	0.60	0.60	0.52	0.39
	Mn	34.7	27.5	9.4	7.6	4.5	26.3	24.6	10.5	7.8	4.8	10.8	3.9
	Mx	48.0	34.2	12.2	9.2	6.5	32.8	31.1	12.4	10.8	7.8	13.0	5.5
E. baverstocki	N	25	24	25	25	25	24	25	25	25	25	25	25
	X	39.6	29.7	10.6	8.4	5.8	28.6	28.0	10.4	8.6	6.6	11.8	4.9
	SD	2.07	2.1	0.65	0.39	0.70	1.44	1.07	0.44	0.45	0.58	0.51	0.38
	Mn	35.4	26.5	9.1	7.5	4.1	26.5	26.0	9.4	7.9	4.8	10.8	3.9
	Mx	43.5	33.8	11.4	9.2	6.8	31.4	31.2	10.9	9.7	7.8	13.0	5.5

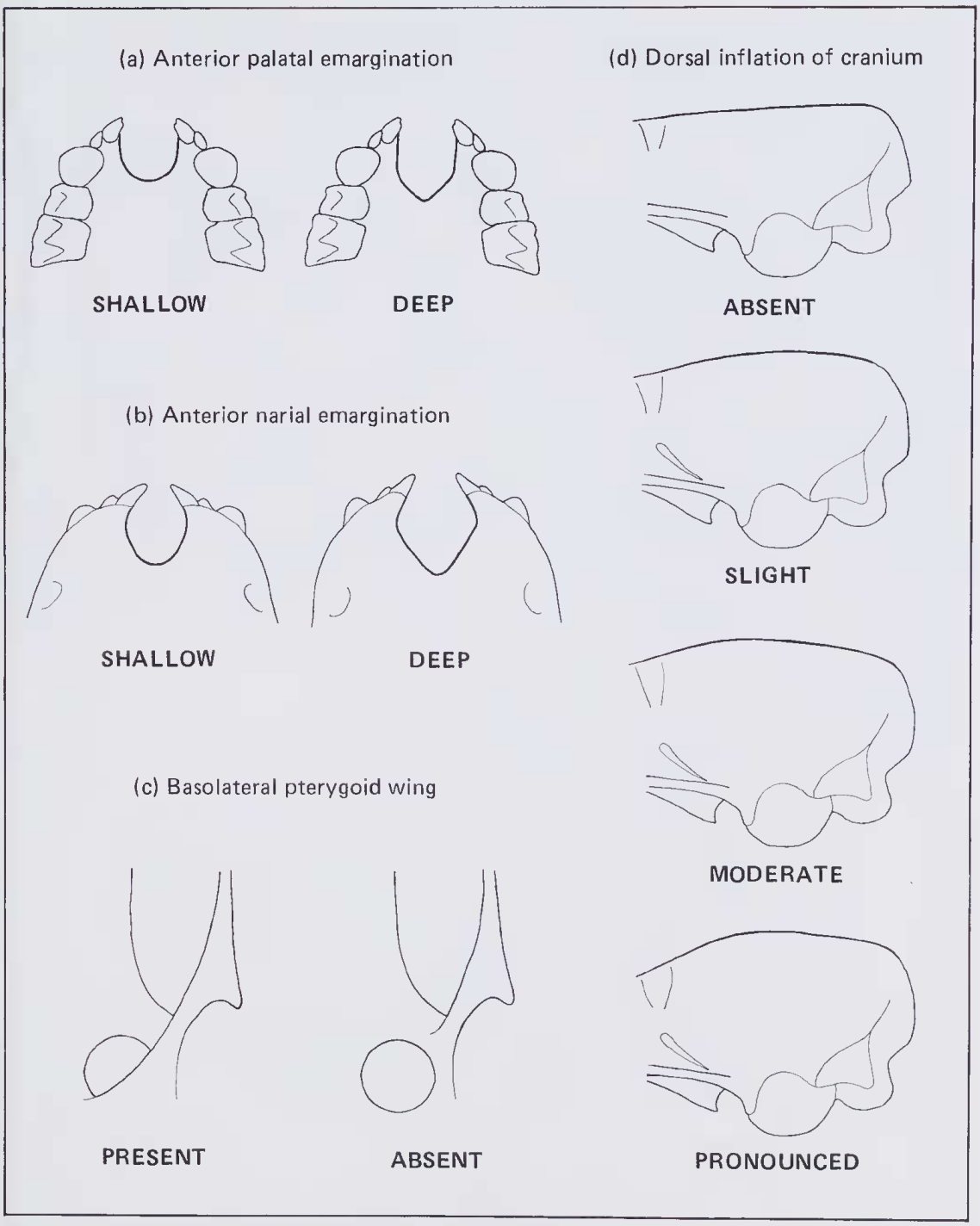


Figure 2 Coded skull characters referred to in text. Further explanation is given in Morphology section of Methods.

Morphometric analyses

Sexual dimorphism was examined using a two factor analysis of variance for measurements of each of the skull, dentary, teeth (skull characters) and external characters for the factors: species-area combinations and sex.

Canonical variate (discriminant) analyses, using both the skull and external measurements, were performed on the species using SPSS (Norusis 1985) and GENSTAT Package, Rothamsted Experimental Station. To obtain an unbiased estimate of the correct classification rate, the canonical variate analyses were repeated using only 80 per cent of the specimens; the canonical variate functions so obtained were then used to classify the remaining 20 per cent of the specimens.

In some of the canonical variate analyses, a Mahalanobis distance matrix was obtained and subjected to a minimum spanning tree analysis and a hierarchical cluster analysis using the unweighted pair group mathematical averaging method (UPGMA).

The above canonical variate and minimum spanning tree cluster analyses were also performed after attempting to correct for size in the 37 variables used. This was done by a principal component analysis of the within-species correlation matrix of the skull and external variables. The latent vectors of this analysis were then examined to determine if the first (and second) vectors had values which suggested that the vector(s) were size vectors. If this was the case then the Principal Component scores associated with these vectors were omitted from the canonical variate and other analyses.

Institutional specimens

To denote the institutional origin of specimens, their catalogue numbers are prefixed by the following abbreviations:

AM	:	Australian Museum, Sydney
AMNH	:	American Museum of Natural History, New York
C	:	Museum of Victoria, Melbourne
CM	:	CSIRO, Australian National Wildlife Collections, Canberra
JM	:	Queensland Museum, Brisbane
SAM	:	South Australian Museum, Adelaide
WAM	:	Western Australian Museum, Perth
EBU	:	Evolutionary Biology Unit, South Australian Museum, Adelaide
NTM	:	Northern Territory Museum, Darwin
BMNH	:	British Museum of Natural History, London

Systematics

Eptesicus Rafinesque, 1820

General Description of Australian *Eptesicus*

Small delicate skulls ranging in greatest length from 10.6 to 14.1 mm; braincase dorsal inflation grades from pronounced in *E. pumilus* and *E. caurinus* through to

absent in *E. baverstocki* sp. nov. (Figure 2d); variation in cranial inflation occurs within some species; sagittal crests absent; lambdoidal crests variably present, never strongly developed; supraorbital tubercles absent to slight, variable within species; postorbital swelling absent or very slight; curve of anterior edge of orbit subcircular, except in *E. darlingtoni* where it is oval; anterior nares outline ranges from broad U to V-shaped, somewhat variable within species, generally not extending posterior to line joining anterior edge of anteorbital foramen; lateral margin of sphenorbital sinus usually a smooth curve except for *E. pumilus* and *E. douglasorum* where it has a noticeable convex inflection; rostrum relatively short, ranges from 48-52 per cent of basicranial length, rostrum width as indicated by anteorbital width ranges from 70-85 per cent of rostrum length; least interorbital width moderate, ranges from 30-36 per cent of basicranial length; infraorbital foramen oval to subcircular, separated from orbit by slight to moderate lacrymal bar; zygomata slender; postpalatal width measured across outside of LM^3 -RM^3 moderately wide, ranging from 48 to 53 per cent of basicranial length; posterior margin of palate (posteropalatal margin of Kitchener *et al.* 1986) conceals openings of posterior nares when viewed vertically; postpalatal spine length small to moderate, shape thin to broadly spatulate; mesopterygoid fossa moderate, sides parallel, only partially conceals sphenorbital sinus; pterygoid process short, hastate, termination of posterior margin of palate ranges from the anterior edge of sphenorbital sinus to approximate mid point of this sinus; anterior palatal emargination variable in shape within species, terminates at a point between the mid point of C^1 and the anterior edge of P^4 ; foramen rotundum moderate, circular or subcircular, partially and variably concealed in some species by a basolateral pterygoid wing (Figure 2c); tympanic bulla moderate, covers two thirds to four-fifths of cochlea, eustachian part small, blunt; anterolateral wings of basioccipital moderate, pressed against edge of cochlea; glenoid fossa rectangular to subcircular; distance between cochlea approximately one-third width of cochlea; paraoccipital process short, does not extend below occipital condyle; anterolateral wing of ectotympanic extends to lateral edge of squamosal in most species except *E. pumilus,* variable in *E. troughtoni* and *E. regulus.* I^1 bilobed, outer cusp shorter than inner cusp, posterior and anterior cingulum slight; I^2 with single cusp, height just above I^1 cingulum to one-quarter height I^1, broad anterolingual basal flange closely pressed against basal part of posterior loph I^1 just below cingulum, anterolateral cingulum slight to moderate, variously with lateral cusplet; diastema between I^2 and C^1 ; C^1 much larger than P^4, posterolingual and posterolabial face slightly to moderately concave, forming a sharp posterior ridge in line with tooth row, encircled by cingulum which is slight on laterolingual surface, loosely contacts P^4 anterior cingulum; P^4 three-quarters height C^1, anterolingual cingular cusplet slight to moderate, anterior and labial cingulum slight to moderate; M^1 paracone shorter than metacone; M^2 paracone subequal in height to metacone; M^3 paracone much higher than M^3 metacone, paracrista length $M^1<M^2<M^3$; mesostyle height M^1 and M^2 subequal $>M^3$; protocone height $M^1>M^2>M^3$; hypocone slight to

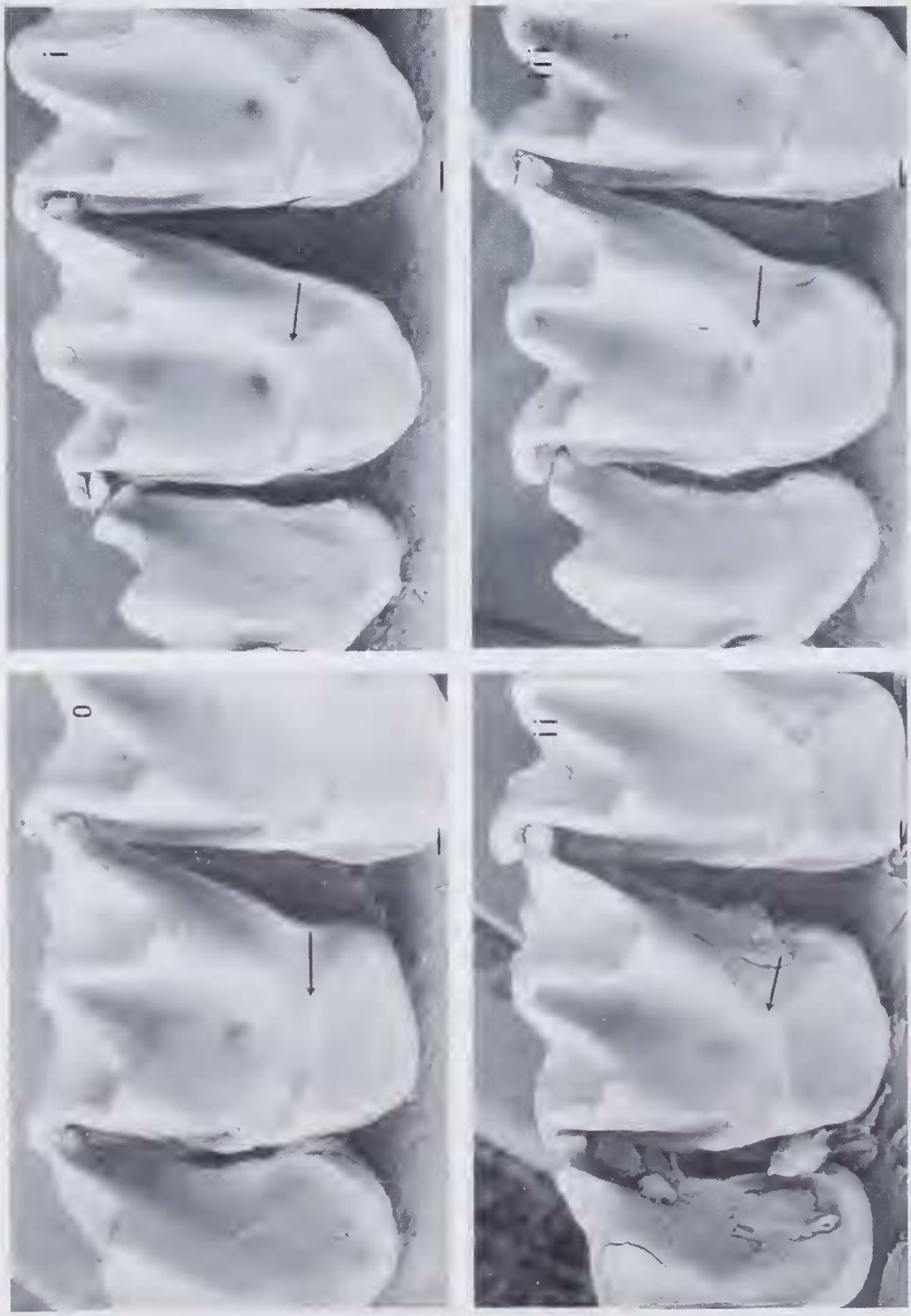


Figure 3 Showing the four grades of development of the metacone-hypocone crista. Illustrated here by an SEM photograph of the first upper molar. The crista is arrowed. Scale line, 100 μm.
(0) absent, (i) slight, (ii) moderate, (iii) large.

moderate; crista linking base of metacone to hypocone M^{1-2} varies from absent to large (Figure 3); anterior, lingual and posterior cingulum well developed M^{1-2}; M^3 anterior and posterolingual cingulum only, moderate; M^{1-3} labial cingulum absent to slight; M^3 lacking metastyle and postmetacrista; upper molar rows parallel or slightly convex.

Dentary moderately dense; angular process beneath or external to condyle; coronoid process sharply or broadly triangular, erect or slightly sloping anteriorly; mental foramen below P_2 or posterior edge C_1; I_{1-3} trilobed, imbricate, approximately equal height; crown area $I_1 < I_2 < I_3$; C_1 tall, in contact with I_3 and P_2, anterior and labial cingulum moderate, posterior and lingual cingulum more developed with slight to pronounced antero – and posterolingual cingular cusplets; P_2 tightly wedged between C_1 and P_4, one-third to one-half C_1 height, encircled with slight to moderate cingulum with slight to moderate antero – posterolingual cusplets; P_4 three quarters height C_1, slight to moderate lingual cingulum with slight to moderate anterolingual cingular cusplet and moderate to absent posterolingual cusplet, labial cingulum slight to moderate; M_{1-3} protoconid and hypoconid decrease in height posteriorly; M_{1-3} paraconid, metaconid and entoconid height subequal, hypoconulid small, hypocristid links hypoconid and entoconid.

The body is small with snout-vent length ranging from 32-50 mm, always longer than tail tip to vent length; ear small, rounded triangular shape, anterior edge smoothly convex, posterior edge concave beneath tip, lower two-thirds smoothly convex; tragus narrow, anterior margin straight or slightly concave, tip rounded, posterior margin convex, posterobasal lobe slight; radius slightly longer or subequal to third metacarpal, length ranges from 26-38 mm; phalanx I/digit III generally shorter, occasionally longer than phalanx II/digit III; phalanx II/digit III longer than phalanx III/digit III; lobe on calcar present or absent, variably developed within species; no colour patterning on fur, dorsal hairs similar colour or darker than ventral hairs, furring of uropatagium varies from well furred to mid point of femur to well furred to knee; patagia usually dark but occasionally a light colour; skin of face and ear varies from usually dark to an occasional light colour.

Glans penis laterally, dorsoventrally or not compressed; urethral opening ventral or terminal; urethral lobe single or bilobed; lateral urethral folds sometimes present, often absent (Figure 4); baculum length varies from 1.6-4.7 mm; dorsal outline rod shaped with expanded base, arrow shaped or dart shaped; lateral profile varies from essentially flat to bow shaped (Figure 5).

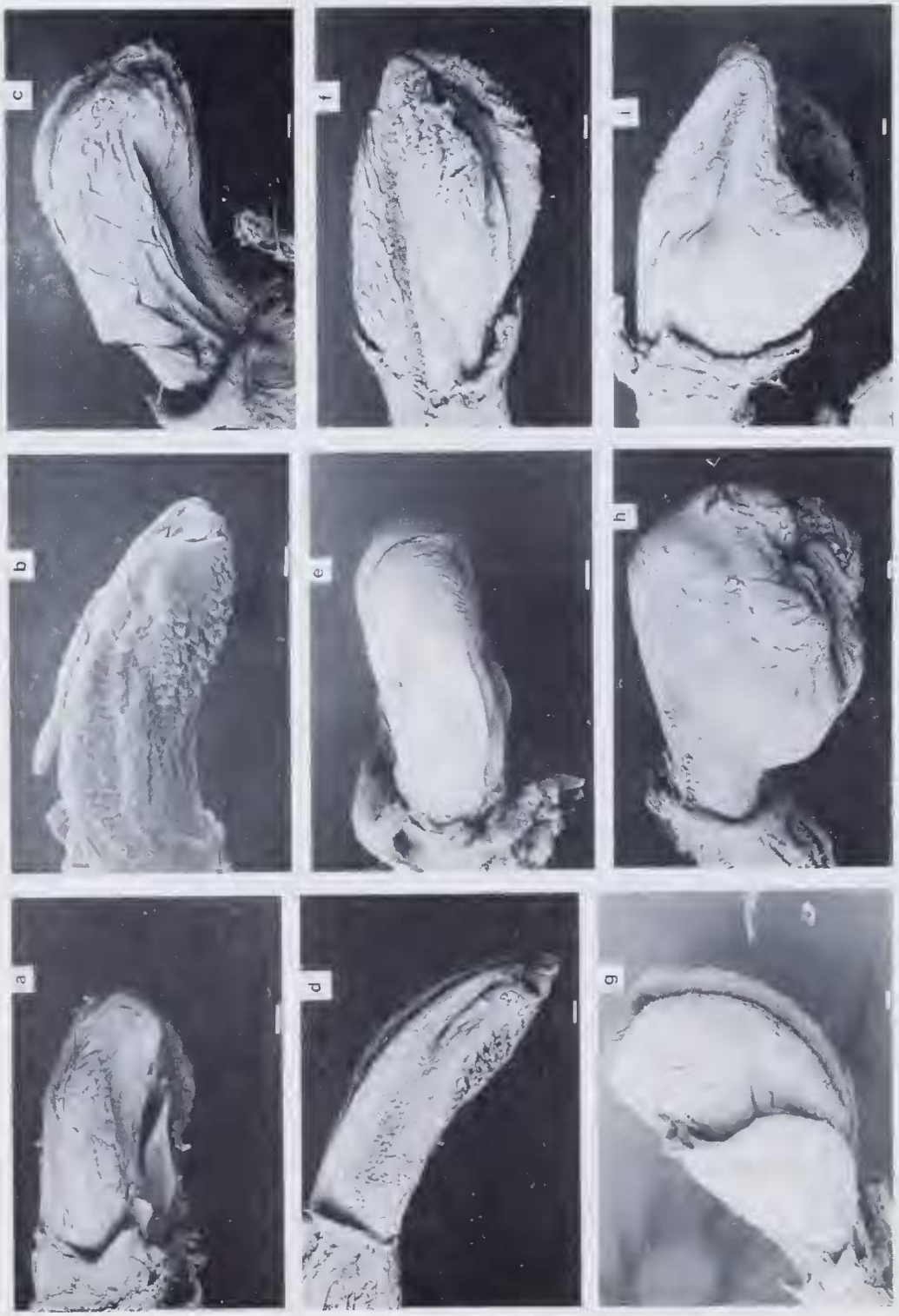


Figure 4 Oblique SEM photographs of the glans penis of the nine species of *Eptesicus*. (a) *E. pumilus*, (b) *E. caurinus*, (c) *E. douglasorum*, (d) *E. finlaysoni*, (e) *E. darlingtoni*, (f) *E. troughtoni*, (g) *E. regulus*, (h) *E. vulturnus* and (i) *E. baverstocki*. Scale lines, 100 μm.

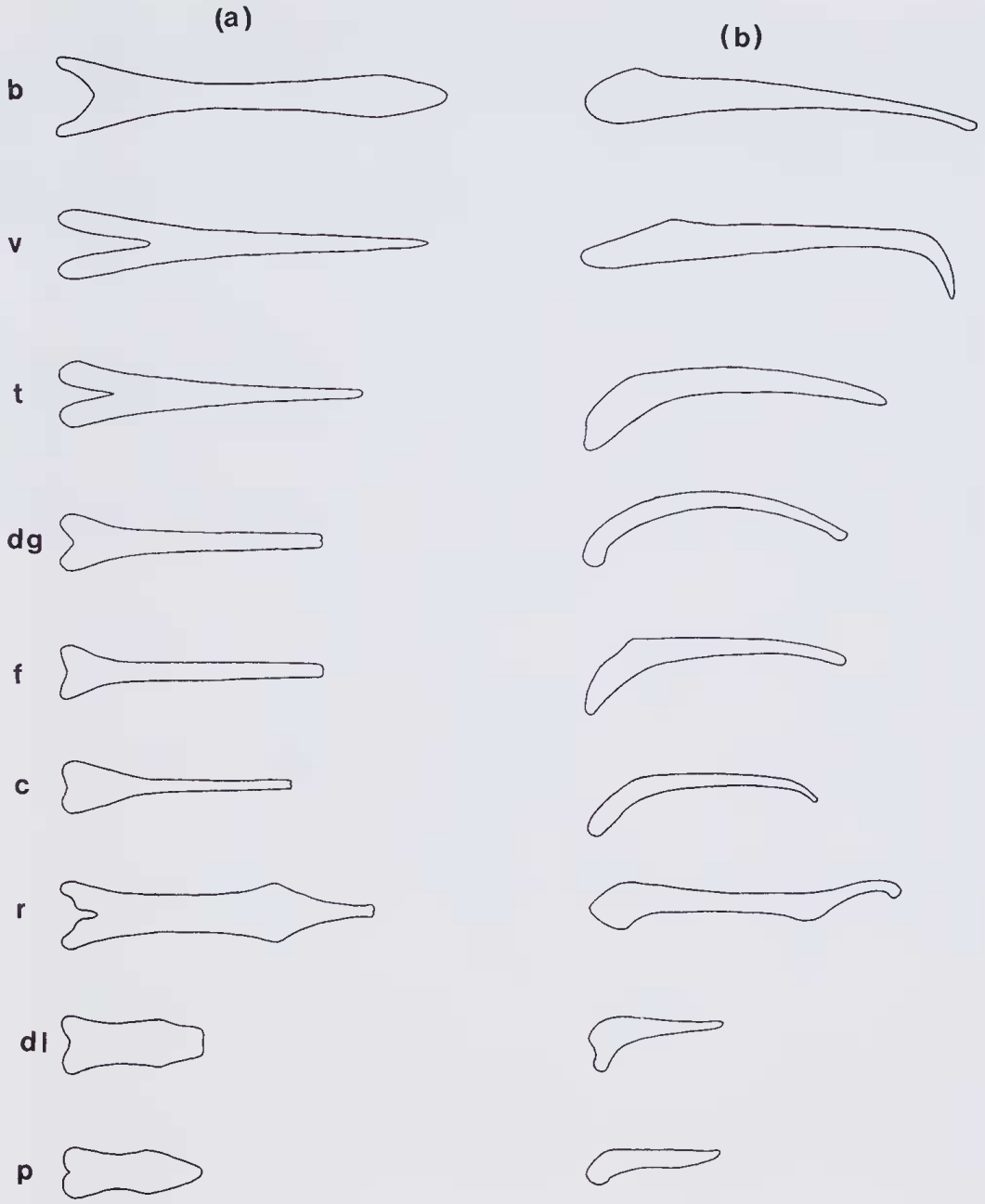


Figure 5 Baculum of the nine species of *Eptesicus*. (a) dorsal view, (b) lateral view. The species code is b, *baverstocki;* v, *vulturnus;* t, *troughtoni;* dg, *douglasorum;* f, *finlaysoni;* c, *caurinus;* r, *regulus;* dl, *darlingtoni;* p, *pumilus.*

Eptesicus pumilus (Gray, 1841)

Figures 4, 5, 6, 7a; Table 1

Scotophilus pumilus Gray, 1841: Journ. Two Exped. Australia (Grey), ii, App., p. 406.

Lectotype (herein designated, see Remarks)

BMNH 41.1523 (119c); adult male; skin and skull (anterior part only); from Yarrundi, on the Dartbrook River, a tributary of the Hunter River, New South Wales (*ca.* 32°00′S, 150°46′E).

Diagnosis (mean values)

Eptesicus pumilus differs from *E. caurinus*: rostrum narrower as indicated by anteorbital, lacrymal and RC^1-LC^1 widths relative to rostrum length (0.73 v. 0.84, 0.96 v. 1.07, 0.71 v. 0.80, respectively); anterior narial emargination deeper; anterolateral wing of ectotympanic further from lateral edge of squamosal; metacone-hypocone crista M^1 absent or slight or rarely moderate, rather than moderate or large; hypocone M^{1-2} larger; manus digit III with phalanx III longer relative to phalanx II (0.87 v. 0.55) and phalanx II shorter relative to phalanx I (0.77 v. 0.95); glans penis dorsoventrally rather than laterally compressed, urethral opening ventral rather than terminal; baculum shorter (1.6 v. 2.9), dorsal outline arrow shaped rather than rod shaped with expanded base, lateral profile less curved.

It differs from *E. douglasorum*: smaller in most skull, dental and external measurements (Table 1); rostrum narrower as indicated by anteorbital, lacrymal and RC^1-LC^1 widths relative to rostrum length (v. 0.83, v. 1.04, v. 0.79, respectively); anterior palatal emargination deeper; anterolateral wing of ectotympanic further from lateral edge of squamosal; metacone-hypocone crista M^1 absent or slight or rarely moderate rather than moderate; hypocone M^{1-2} larger; manus digit III with phalanx III longer relative to phalanx II (v. 0.54), and phalanx II much shorter relative to phalanx I (v. 1.04); skin of face, ears and radius darker; glans penis dorsoventrally rather than laterally compressed, urethral opening ventral rather than terminal; baculum shorter (v. 3.2), dorsal outline arrow shaped rather than rod shaped with expanded base, lateral profile less curved.

It differs from *E. finlaysoni*: smaller in most skull, dental and external measurements (Table 1); dorsal inflation of cranium pronounced rather than slight or moderate; rostrum narrower as indicated by anteorbital, lacrymal and RC^1-LC^1 widths relative to rostrum length (v. 0.82, v. 1.08, v. 0.80, respectively); anterior narial and palatal emarginations usually deeper; anterolateral wing of ectotympanic further from lateral edge of squamosal; manus digit III with phalanx III longer relative to phalanx II (v. 0.60) and phalanx II shorter relative to phalanx I (v. 0.91); glans penis dorsoventrally rather than laterally compressed, urethral opening ventral rather than terminal; baculum shorter (v. 3.1), dorsal outline arrow shaped rather than rod shaped with expanded base, lateral profile less curved.

It differs from *E. darlingtoni*: smaller in all skull, dental and external measurements (Table 1); dorsal inflation of cranium pronounced rather than slight or moderate; anterior narial emargination shallow rather than deep, anterior palatal emargination shallow rather than generally deep; sphenorbital sinus with lateral margin more smoothly curved; anterolateral wing of ectotympanic further from lateral edge of squamosal; manus digit III with phalanx III shorter relative to phalanx II (v. 0.92); baculum dorsal outline similar but distally pointed rather than square, base slopes more posteriorly in lateral profile.

It differs from *E. troughtoni*: smaller in most skull, dental and external measurements (Table 1); dorsal inflation of cranium pronounced rather than moderate; rostrum narrower as indicated by anteorbital, lacrymal and RC^1-LC^1 widths relative to rostrum length (v. 0.81, v. 1.06, v. 0.77, respectively); anterior palatal emargination deeper, outline oval rather than U shaped; manus digit III with phalanx III longer relative to phalanx II (v. 0.67) and phalanx II shorter relative to phalanx I (v. 0.87); glans penis dorsoventrally rather than laterally compressed, urethral opening ventral rather than terminal; baculum shorter (v. 3.7), dorsal outline arrow shaped rather than rod shaped with expanded base, lateral profile less curved.

It differs from *E. regulus*: dorsal inflation of cranium pronounced rather than absent to moderate; basolateral pterygoid wing present, rather than usually absent; anterior palatal emargination narrower, usually shallower; glans penis dorsoventrally compressed, urethral lobe small, simple, lacks lateral urethral folds; baculum shorter (v. 3.8), dorsal outline arrow rather than elongate dart shaped.

It differs from *E. vulturnus*: dorsal inflation of cranium pronounced rather than slight or absent; basolateral pterygoid wing present rather than usually absent; anterior palatal emargination narrower, usually shallower; postpalatal spine generally smaller; posterior margin of palate well posterior to anterior edge of sphenorbital sinus; anterolateral wing of ectotympanic further from lateral edge of squamosal; glans penis dorsoventrally compressed rather than bulbous, urethral opening ventral rather than terminal; baculum much shorter (v. 4.4), dorsal outline arrow shaped rather than rod shaped with expanded base.

It differs from *E. baverstocki*: dorsal inflation of cranium pronounced rather than slight or absent; basolateral pterygoid wing present; anterior palatal emargination narrower; postpalatal spine generally smaller; posterior margin of palate well posterior to anterior edge of sphenorbital sinus; anterolateral wing of ectotympanic further from lateral edge of squamosal; manus digit III with phalanx III longer relative to phalanx II (v. 0.78) and phalanx II shorter relative to phalanx I (v. 0.84); glans penis dorsoventrally compressed rather than funnel shaped, ventral urethral lobe single rather than bilobed; baculum much shorter (v. 4.7), base more deflected ventrally, dorsal outline arrow shaped rather than rod shaped with slight distal lateral wings and expanded base.

Description

Skull (Figure 6)

(see also 'General Description of Australian *Eptesicus*'). Greatest length short 12.1 (11.3-12.7); cranial inflation pronounced; lamdoidal crest slight to moderate; anterior narial emargination usually V-shaped, occasional narrow U-shaped, terminates well anterior to a line joining anterior edge of anteorbital foramina; rostrum long, averages 51.5 per cent of basicranial length; least interorbital distance wide, averages 35.6 per cent of basicranial length; anteorbital distance narrow averages 73.1 per cent of rostrum length; inter upper third molar distance moderate, averages 50.5 per cent of basicranial length; lacrymal bar moderately wide to wide; postpalatal spine broad to narrow spatulate, short; posterior margin of palate terminates well posterior to anterior edge of sphenorbital sinus; basolateral pterygoid wing covers foramen rotundum to the following extent: less than one-third (75 per cent) or between one – to two-thirds (25 per cent).

Dentition

Crista linking base of metacone and hypocone on M^1 absent (46 per cent) or slight (46 per cent) or moderate (8 per cent) and on M^2 absent (71 per cent) or slight (29 per cent).

Body size

Body length moderate 39.1 (35.0-44.2), much longer than tail 30.7 (27.6-33.0); relative wing measurements as follows: RL moderate 30.6 (28.1-32.9)>MCIII>> P1>P2>P3; tibia length small 12.6 (11.6-13.8).

Pelage and skin

Dorsal pelage medium dark with paler ventral surface. Hair on top of head and face monocoloured, Bister; cheeks, chin, anal region and patagia Snuff Brown and ears Bister; on neck have distal one-quarter Snuff Brown and base Clove Brown; on dorsum *ca.* 4.5 mm long, distal one-third Olive Brown and base Clove Brown; on chest, venter and sides of body distal one-quarter Snuff Brown and base Clove Brown; proximal one-third of humerus with sparse hairs; uropatagium lightly furred; plagiopatagium furred to *ca.* 4 mm from side of body. Skin of lips Wood Brown and of ear, radius and patagia Clove Brown.

Penis (Figure 5)

Long hairs, up to 3.3 mm on preputium; preputial skin attached to glans *ca.* 1.0 mm from distal end; glans dorsoventrally compressed; urethral opening in mid ventral region of head of glans, covered by upward triangular projection of skin from ventral margin of opening, dorsal outline obovate shape; dorsal surface of head of glans with shallow median longitudinal groove; lateral profile of glans a blunt rod shape.

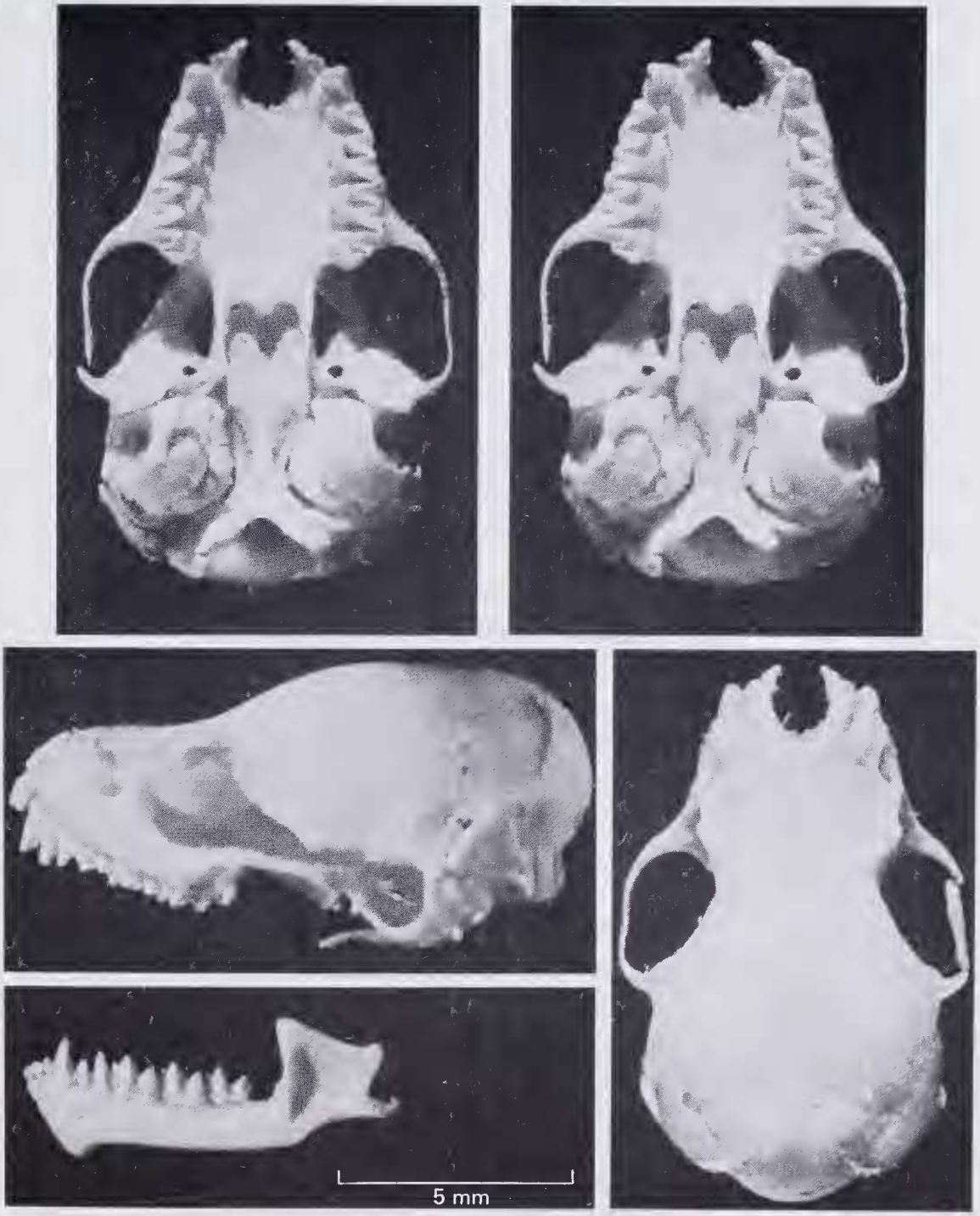


Figure 6 Skull and dentary of *Eptesicus pumilus* (EBU 006). The ventral view are stereopairs. Scale line 5 mm.

Figure 7 Distribution maps of the nine species of *Eptesicus*. (a) *pumilus*, (b) *caurinus*, (c) *douglasorum*, (d) *finlaysoni*, (e) *darlingtoni*, (f) *troughtoni*, (g) *regulus*, (h) *vulturnus*, (i) *baverstocki*. ●, localities of measured specimens. ○, localities of referred specimens. Geographic groups are numbered.

Baculum (Figure 4)

Baculum very short, dorsal outline arrow shaped, greates length 1.63 ± 0.111 (SD)(N=7) and basal width 0.64 ± 0.053 (SD)(N=7); lateral profile moderately flat, base with slightly thickened dorsoventral inflection.

Distribution

East of the Great Dividing Range, between latitudes 18° and 33°S. In vegetation which covers the broad categories of subtropical rainforest and dry and wet sclerophyll forest (Figure 7a).

Remarks

Gray (1841) did not designate a holotype in his description of *Scotophilus pumilus* collected at Yarrundi, New South Wales. Dobson (1878) lists as the 'type' a specimen (adult, skin) from Australia "Figured in Voy. Erebus and Terror". Tate (1942) referred to the 'type' skull as BM. 41.1523(119c) from Yarrundi. This specimen is a skin and damaged skull from Yarrundi. Its label has written on it "lectotype, 1914" – perhaps by Oldfield Thomas. However, until now, this specimen has not been formerly designated a lectotype.

Specimens examined

Lectotype

BMNH 41.1523(119c)

New South Wales: Acacia Plateau (28°20'S, 152°18'E) 1 ♀, 2 ♂, EBU (B341-3); Border Range National Park (28°20'S, 153°00'E) 4 ♀, 5 ♂, AM13168, AM13179-80, AM13183-4, AM13187, AM13257, AM13262, AM13408; Coopernook State Forest (31°50'S, 152°36'E) 1 ♀, EBU006; Iluka Nature Reserve (29°24'S, 153°22'E) 1 ♂, AM13190; Newcastle (33°00'S, 151°19'E) 1 ♂, EBU004; New England National Park (*ca.* 30°30'S, 152°36'E) 1 ♀, AM13201; Nightcap National Park (28°35'S, 153°18'E) 2 ♀, 1 ♂, AM13233, AM13237, AM13242; "Sydney" 1 ♂, BM62.10.26.10; Watagan State Forest (33°00'S, 151°19'E) 1 ♂, B354; near Byron Bay (28°40'S, 153°32'E) 1 ♀, 1 ♂, EBU (008-9); Woolgoolga Flora Reserve (30°07'S, 153°09'E) 1 ♂, AM13266.

Queensland: Kirrama State Forest (18°10'S, 145°40'E) 1 ♂, EBU070.

Eptesicus caurinus Thomas, 1914

Figures 4, 5, 7b, 8; Table 1

Eptesicus pumilus caurinus Thomas, 1914: Ann. Mag. Nat. Hist. (8) xiii, p. 439.

Holotype

BMNH 14.3.9.1.10473; adult male; body in ethanol, skull separate; from Drysdale, Kimberley, Western Australia; collected by G.F. Hill.

Diagnosis (mean values)

Eptesicus caurinus differs from *E. pumilus* in having rostrum broader as indicated by anteorbital, lacrymal and RC^1-LC^1 widths relative to rostrum length

(0.84 v. 0.73, 1.07 v. 0.96, 0.80 v. 0.71, respectively); anterior narial emargination shallower; anterolateral wing of ectotympanic closer to lateral edge of squamosal; metacone-hypocone crista M^1 moderate or large rather than absent or slight or rarely moderate; hypocone M^{1-2} smaller; manus digit III with phalanx III shorter relative to phalanx II (0.55 v. 0.87) and phalanx II longer relative to phalanx I (0.95 v. 0.77); glans penis laterally rather than dorsoventrally compressed, urethral opening terminal rather than ventral; baculum longer (2.9 v. 1.6), dorsal profile rod shaped with expanded base rather than arrow shaped, lateral profile more curved.

It differs from *E. douglasorum*: much smaller in all skull, dental and external measurements (Table 1); anterior narial emargination deeper; manus digit III with phalanx I shorter relative to metacarpal (0.32 v. 0.37); skin of face, ears and radius darker; baculum generally shorter (v. 3.2), less curved in lateral profile.

It differs from *E. finlaysoni*: metacone-hypocone crista M^1 moderate or large rather than absent or slight or very rarely moderate; interorbital region generally broader relative to basicranial length (0.36 v. 0.32); baculum generally shorter (v. 3.1).

It differs from *E. darlingtoni*: much smaller in most skull, dental and external measurements (Table 1); curve of anterior edge of orbit subcircular rather than oval; rostrum broader as indicated by anteorbital, lacrymal and RC^1-LC^1 widths relative to rostrum length (v. 0.72, v. 0.96, v. 0.74, respectively); anterior narial emargination shallow rather than deep; anterior palatal emargination shallower; metacone-hypocone crista M^1 moderate or large rather than absent or slight; hypocone M^{1-2} smaller; manus digit III with phalanx III much shorter relative to phalanx II (v. 0.92) and phalanx II longer relative to phalanx I (v. 0.74); glans penis laterally rather than dorsoventrally compressed, urethral opening terminal rather than ventral; baculum longer (v. 3.1), dorsal outline rod shaped with expanded base rather than blunt arrow shaped, more curved in lateral profile.

It differs from *E. troughtoni*: smaller in all skull, dental and external measurements (Table 1); anterior palatal emargination usually narrower; metacone-hypocone crista M^1 moderate or large rather than absent to moderate; hypocone M^{1-2} smaller; glans penis more pointed distally, much narrower dorsoventrally urethral opening terminal rather than ventral; baculum shorter (v. 3.7), basal notch shorter.

It differs from *E. regulus*: smaller in most skull, dental and external measurements (Table 1); dorsal inflation of cranium pronounced or moderate rather than slight or absent; basolateral pterygoid wing present rather than absent; anterior part of rostrum broader as indicated by anteorbital and RC^1-LC^1 widths relative to rostrum length (v. 0.76, v. 0.74, respectively); anterior narial and palatal emarginations shallower, usually narrower; upper tooth row more curved; metacone-hypocone crista M^1 moderate or large rather than absent or slight or rarely moderate; hypocone M^{1-2} smaller; manus digit III with phalanx III shorter relative to phalanx II (v. 0.80) and phalanx II longer relative to phalanx I (v. 0.87); glans

penis much narrower dorsoventrally, urethral opening terminal rather than ventral, lacks lateral urethral folds; baculum shorter (v. 3.8), dorsal outline rod shaped with expanded base rather than elongate dart shaped, curved rather than essentially flat in lateral profile.

It differs from *E. vulturnus*: smaller in most skull and dental measurements (Table 1); dorsal inflation of cranium pronounced or moderate rather than absent or slight; basolateral pterygoid wing present; anterior part of rostrum broader as indicated by anteorbital and RC^1-LC^1 widths relative to rostrum length (v. 0.75, v. 0.75, respectively); anterior narial and palatal emarginations narrower, usually shallower; posterior margin of palate terminates well posterior to anterior edge of sphenorbital sinus; upper toothrow more curved; metacone-hypocone crista M^1 moderate or large rather than absent or slight; hypocone M^{1-2} smaller; manus digit III with phalanx III shorter relative to phalanx II (v. 0.80) and phalanx II longer relative to phalanx I (v. 0.78); glans penis distally pointed rather than blunt, narrow dorsoventrally rather than bulbous, ventral urethral lobe a single fleshy tongue rather than two subcircular winged lobes; baculum much shorter (v. 4.4), distal tip less curved ventrally.

It differs from *E. baverstocki*: smaller in most skull and dental measurements (Table 1); dorsal inflation of cranium moderate or pronounced rather than absent or slight; basolateral pterygoid wing present; rostrum broader anteriorly as indicated by anteorbital and RC^1-LC^1 widths relative to rostrum length (v. 0.76, v. 0.78, respectively); anterior narial and palatal emarginations narrower and shallower; posterior margin of palate well posterior to anterior edge of sphenorbital sinus; upper tooth row usually more curved; metacone-hypocone crista M^1 moderate or large rather than absent; hypocone M^{1-2} smaller; manus digit III with phalanx III shorter relative to phalanx II (v. 0.78) and phalanx II longer relative to phalanx I (v. 0.84); glans penis distally pointed rather than funnel shaped, ventral urethral lobe a single fleshy tongue rather than bilobed; baculum much shorter (v. 4.7), more curved in lateral profile.

Description

Skull (Figure 8)

(see also 'General Description of Australian *Eptesicus*'). Greatest skull length short 11.2 (10.6-12.0); cranial inflation moderate (59 per cent) or pronounced (41 per cent); lambdoidal crest slight to moderate; anterior narial emargination usually V-shaped, occasionally U-shaped, usually terminates close to (94 per cent) or well anterior to (6 per cent) a line joining anterior edge of anteorbital foramina; rostrum short, averages 47.8 per cent basicranial length; least interorbital distance wide, averages 35.1 per cent basicranial length; anteorbital distance wide, averages 84.4 per cent rostrum length; inter upper third molar distance moderate, averages 51.1 per cent basicranial length; lacrymal bar narrow to moderate; postpalatal spine broad to narrow spatulate or broadly triangular, long; posterior margin of palate terminates well posterior to anterior edge of sphenorbital sinus; basolateral

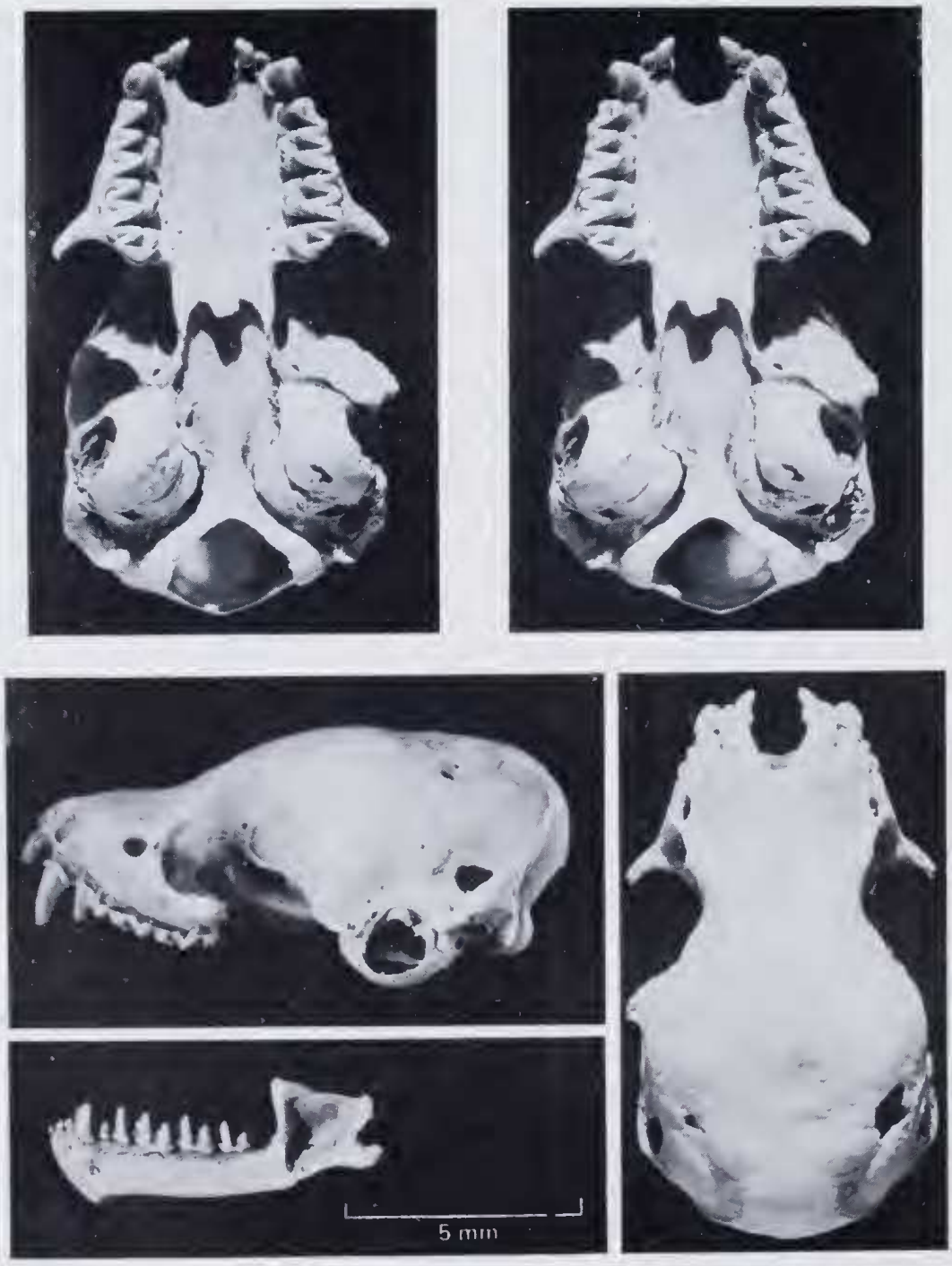


Figure 8 Skull and dentary of *Eptesicus caurinus* (WAM M17367, paratype). The ventral view are stereopairs. Scale line 5 mm.

pterygoid wing coverage of foramen rotundum less than one-third (19 per cent) or between one and two-thirds (68 per cent) or more than two-thirds (13 per cent).

Dentition

Crista linking base of metacone and hypocone on M^1 moderate (59 per cent) or large (41 per cent) and M^2 slight (9 per cent) or moderate (69 per cent) or large (22 per cent)

Body size

Body length small 36.7 (32.1-40.0), much longer than tail length 30.2 (24.4-34.8); relative wing measurements as follows: RL small 29.5 (26.6-31.7)>MCIII >>P1>P2>>P3; tibia length moderate 11.4 (10.7-12.4).

Pelage and skin

Dorsal pelage moderately pale with pale ventral surface. Hair on top of head has distal one-third Dresden Brown and base Chaetura Black; cheeks Isabella Color; face, chin, neck have distal one-quarter to two-thirds Isabella Color and base Chaetura Black; on dorsum *ca.* 5.5 mm long, distal one-quarter Isabella Color and base Chaetura Black; chest has distal one-quarter Isabella Color and base Chaetura Black; on venter *ca.* 5.2 mm long, distal one-quarter Cream Buff and base Chaetura Black; anal region has distal three-quarters Ivory Yellow and base Chaetura Black; sides of body Cream Buff; humerus sparsely haired to elbow, Ivory Yellow; femur furred to half length, Ivory Yellow; ear haired to one-third length, Cream Buff; uropatagium very sparsely furred, Ivory Yellow; plagiopatagium very sparsely furred to 2.5 mm from side of body. Skin of lips Fuscous Black; ear and patagia Fuscous and radius Bister.

Penis (Figure 4)

Long hairs up to 3 mm on preputium; preputial skin attached to glans at base of head *ca.* 1.5 mm from distal end; head of glans laterally compressed; urethral opening at distal end of glans, covered by upward projecting narrow tongue of skin from ventral lip of opening; dorsal surface of head of glans with deep median longitudinal groove, ventral surface with slight ventral keel; slight anterolateral elliptical swellings above ventral keel, covered with numerous very small spines, lateral profile an opiculate shape.

Baculum (Figure 5)

Moderately long, greatest length 2.86 ± 0.158 (SD)(N=10); dorsal outline rod shaped, proximal one-third gently expanded into a slightly bifurcated base with width 0.67 ± 0.095 (SD)(N=10); base and distal end gently curved ventrally – the base more so.

Distribution

More rugged terrain of the Kimberley district, Western Australia and northern parts of the Northern Territory. In vegetation which covers the broad categories of mixed tropical woodland and tropical layered woodland (Figure 7b).

Specimens examined

BMNH 14.3.9.1.10473 (holotype).

Northern Territory: Borroloola (16°04'S, 136°18'E) 2 ♂, C5216-7; Delamere Crk (15°51'S, 131°35'E) 1 ♀, NTM539; Jasper Gorge (16°02'S, 130°45'E) 4 ♀, 1 ♂, EBUB233-7; Keep R. (15°46'S, 129°05'E) 1 ♂, NTM540, (15°47'S, 129°06'E) 1 ♀, 1 ♂, NTM (549,557); Mt Brockman (12°45'S, 132°56'E) 1 ♂, CM4667; Nourlangie (12°46'S, 132°39'E) 1 ♂, CM4629; 70 km E Pine Crk (13°35'S, 132°15'E) 1 ♂, EBUB193; Skull Crk Major (*ca.* 15°44'S, 130°46'E) 4 ♀, EBUB223-6.

Western Australia: Barker Gorge (17°15'20"S, 124°43'45"E) 1 ♂, WAM18538; Beverley Springs (16°39'30"S, 125°30'00"E) 1 ♂, WAM18487; Drysdale R. (*ca.* 14°45'S, 126°57'E) 1 ♂, WAM17367 (paratype); Drysdale R. National Park (15°03'S, 126°44'E) 1 ♂, WAM14009; Geike Gorge (18°05'S, 125°43'E) 2 ♀, CM125-6; Kununnurra (15°46'S, 128°48'E) 2 ♀, 1 ♂, EBUC128-9, CM4495; Lennard R. Gorge (17°10'50"S, 125°11'30"E) 1 ♂, WAM18539; Mitchell Plateau (14°53'40"S, 125°45'20"E) 1 ♀, 1 ♂, WAM (15756, 15758), (14°35'00"S, 125° 43'15"E) 1 ♂, WAM18420; Parry Crk (15°38'S, 128°18'E) 1 ♀, 1 ♂, WAM19339-40; Spillway Cave (16°02'30"S, 128°44'30"E) 1 ♀, 1 ♂, WAM (11569, 11574); Tunnel Crk (17°36'30"S, 125° 08'40"E) 2 ♀, WAM (24050, 24053); Wotjulum Mission (16°11'S, 123°37'E) 2 ♀, 1 ♂, WAM3009-11.

Eptesicus douglasorum Kitchener, 1976

Figures 4, 5, 7c, 9; Table 1

Eptesicus douglasi Kitchener, 1976: Rec. West. Aust. Mus. 4: 295-301.

Holotype

WAM M3405C (= M3405.003); adult male; body in ethanol, skull separate; from Tunnel Creek, Napier Range, Western Australia (17°37'S, 125°09'E) at altitude *ca.* 140 m; mist-netted by D. Farner and D.L. Serventy on 10 October 1958 at entrance of cave.

Diagnosis (mean values)

Eptesicus douglasorum differs from *E. pumilus*: larger in most skull, dental and external measurements (Table 1); rostrum broader as indicated by anteorbital, lacrymal and RC^1-LC^1 widths (0.83 v. 0.73, 1.04 v. 0.96, 0.79 v. 0.71, respectively); anterior palatal emargination shallower; anterolateral wing of eetotympanie nearer to lateral edge of squamosal; metaeone-hypocone erista M^1 moderate rather than absent or slight or rarely moderate; hypoeone M^{1-2} smaller; manus digit III with phalanx III shorter relative to phalanx II (0.54 v. 0.87) and phalanx II mueh longer relative to phalanx I (1.04 v. 0.77); skin of face, ears and radius lighter; glans penis laterally rather than dorsoventrally compressed, urethral opening terminal rather than ventral; baeulum longer (3.2 v. 1.6), lateral profile more eurved, dorsal outline rod shaped with expanded base rather than arrow shaped.

It differs from *E. caurinus*: much larger in all skull, dental and external measurements (Table 1); anterior narial emargination generally shallower; manus digit III with phalanx I shorter relative to metaearpal (0.32 v. 0.37); skin of faee, ears and radius lighter; baeulum generally longer (v. 2.9).

It differs from *E. finlaysoni*: metacone-hypocone crista M^1 moderate rather than absent or slight; hypocone M^{1-2} smaller; manus digit III with phalanx I shorter relative to metacarpal (v. 0.38); skin of face, ears and radius lighter; baculum more curved in lateral profile.

It differs from *E. darlingtoni*: anterior narial and palatal emarginations shallow rather than deep; dorsal inflation of cranium pronounced or moderate rather than slight or moderate; curve of anterior edge of orbit more even, subcircular; metacone-hypocone crista M^1 moderate rather than absent to slight; hypocone M^{1-2} smaller; manus digit III with phalanx III much shorter relative to phalanx II (v. 0.92) and phalanx II much longer relative to phalanx I (v. 0.74); skin of face, ears and radius lighter; glans penis laterally rather than dorsoventrally compressed, urethral opening terminal rather than ventral; baculum much longer (v. 1.7), dorsal outline rod shaped with expanded base rather than blunt arrow shaped, more curved in lateral profile.

It differs from *E. troughtoni*: anterior narial emargination narrower; hypocone M^{1-2} smaller; manus digit III with phalanx II longer relative to phalanx I (v. 0.87) and phalanx I shorter relative to metacarpal (v. 0.37); skin of face, ears and radius lighter; glans penis more pointed distally; baculum shorter (v. 3.7).

It differs from *E. regulus*: dorsal inflation of cranium moderate or pronounced rather than slight or absent; basolateral pterygoid wing present rather than usually absent; rostrum broader anteriorly as indicated by anteorbital and RC^1-LC^1 widths relative to rostrum length (v. 0.76, v. 0.74, respectively); anterior narial and palatal emarginations narrower, shallower; upper tooth row more curved; metacone-hypocone crista M^1 moderate rather than slight or absent or occasionally moderate; hypocone M^{1-2} smaller; manus digit III with phalanx III shorter relative to phalanx II (v. 0.80) and phalanx II longer relative to phalanx I (v. 0.81); glans penis more pointed distally, urethral opening terminal rather than ventral, lateral urethral folds absent; baculum shorter (v. 3.8), dorsal outline rod shaped with expanded base rather than elongate dart shaped, lateral profile curved rather than flat.

It differs from *E. vulturnus*: larger in most skull, dental and external measurements (Table 1); dorsal inflation of cranium moderate or pronounced rather than slight or absent; basolateral pterygoid wing present; rostrum broader anteriorly as indicated by anteorbital and RC^1-LC^1 widths relative to rostrum length (v. 0.75, v. 0.75, respectively); anterior palatal emargination narrower; posterior margin of palate terminates well posterior to anterior edge of sphenorbital sinus; metacone-hypocone crista M^1 moderate rather than slight or absent; hypocone M^{1-2} smaller; manus digit III with phalanx III shorter relative to phalanx II (v. 0.80) and phalanx II longer relative to phalanx I (v. 0.78); glans penis distally pointed rather than blunt, ventral urethral lobe with a pronounced tongue-like projection rather than two small subcircular winged lobes; baculum shorter (v. 4.4), lateral profile bow shaped rather than distally curved.

It differs from *E. baverstocki*: larger in most skull, dental and external measurements (Table 1); dorsal inflation of cranium moderate or pronounced rather than

absent or slight; basolateral pterygoid wing present; anterior palatal emargination broader; posterior margin of palate well posterior to anterior edge of sphenorbital sinus; metacone-hypocone crista M^1 moderate rather than absent; hypocone M^{1-2} smaller; manus digit III with phalanx III shorter relative to phalanx II (v. 0.78) and phalanx II longer relative to phalanx I (v. 0.84); glans penis distally pointed rather than funnel shaped, ventral urethral lobe single rather than bilobed; baculum shorter (v. 4.7), distal end more curved ventrally.

Description

Skull (Figure 9)

(see also 'General Description of Australian *Eptesicus*'). Greatest skull length moderately long 12.8 (12.3-13.2); cranial inflation moderate (55 per cent) or pronounced (45 per cent); lambdoidal crest slight to moderate; anterior narial emargination generally V-shaped, occasionally U-shaped, terminates anterior to a line joining anterior edge of anteorbital foramina; rostrum short, averages 48.6 per cent of basicranial length; least interorbital distance narrow, averages 32.1 per cent basicranial length; anteorbital distance wide, averages 83.0 per cent of rostrum length; inter upper third molar distance moderate, averages 50.4 per cent basicranial length; lacyrmal bar moderate to wide; postpalatal spine broad to narrow spatulate and moderately long; posterior margin of palate terminates well posterior to anterior edge of sphenorbital sinus; basolateral pterygoid wing coverage of foramen rotundum: less than one-third (27 per cent) or between one and two-thirds (55 per cent) or more than two-thirds (18 per cent).

Dentition

Crista linking base of metacone and hypocone on M^1 moderate and on M^2 slight (18 per cent) or moderate (64 per cent) or large (18 per cent).

Body size

Body length moderate 39.7 (35.3-43.5), longer than tail 36.3 (35.2-37.9); relative wing measurements as follows: RL very large 36.2 (34.3-37.6)>MCIII>> P1≤P2>>P3; tibia length large 14.3 (13.6-15.5).

Pelage and skin

Overall pelage pale grey. Hair on top of head has distal one-half Drab Gray or Pale Orange and base Chaetura Black; cheeks, face and chin Drab Gray or Pale Orange; neck with distal one-quarter Pale Drab Gray and base Chaetura Black; on dorsum *ca.* 5.3 mm long, distal one-quarter Light Drab and base Chaetura Black; on chest and venter *ca.* 4.5 mm long, distal one-half Drab Gray or Pale Olive Buff and base Chaetura Black or Clove Brown; anal region Pale Drab Gray; sides of body with distal one-third Drab Gray and base Chaetura Black; humerus and femur sparsely haired for half their length, Pale Drab Gray; ear one-third furred, Light Drab; uropatagium very sparsely haired on proximal two-thirds; plagiopatagium very sparsely haired *ca.* 8 mm from side of body. Skin of lips Light

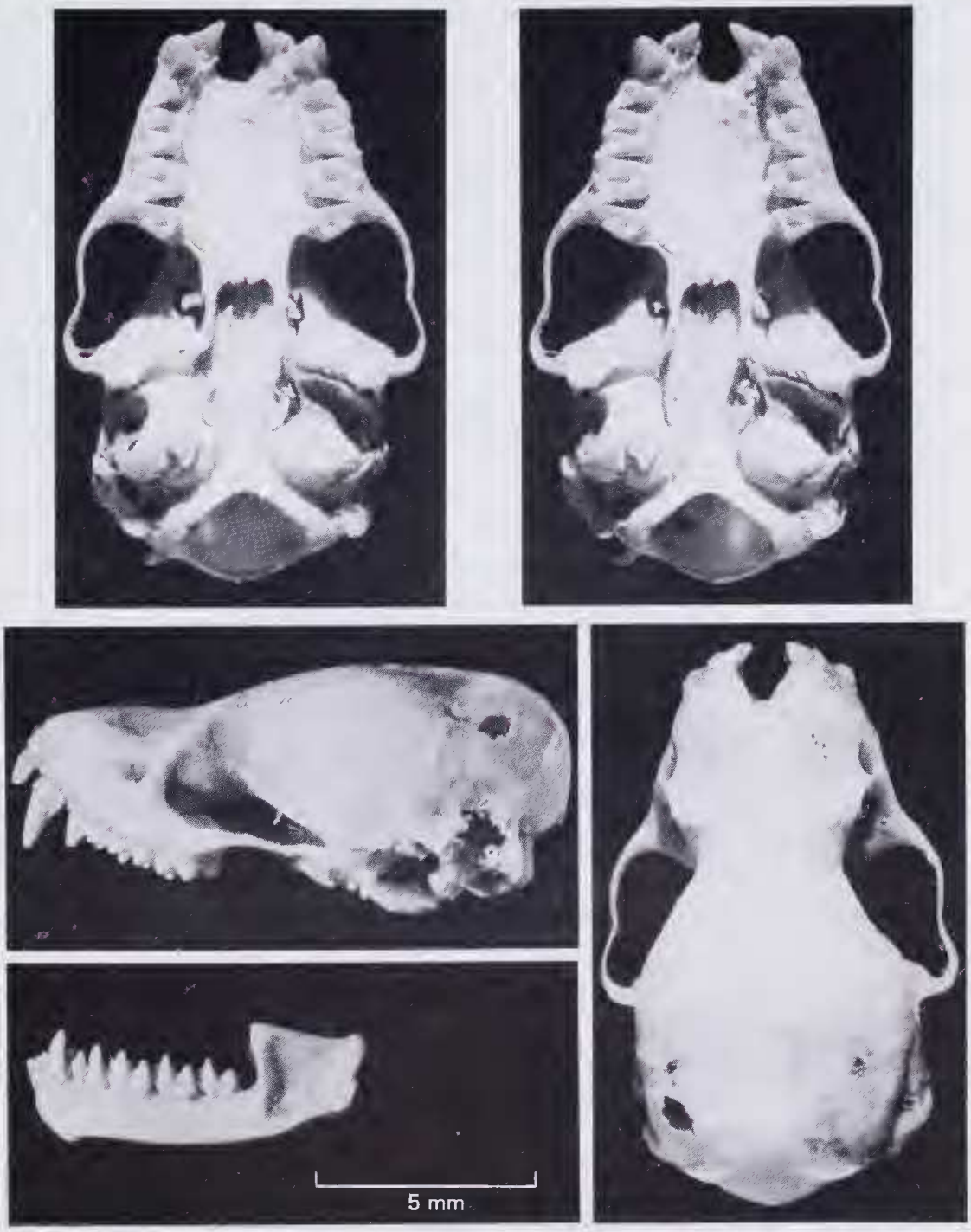


Figure 9 Skull and dentary of *Eptesicus douglasorum* (WAM M3405C, holotype). The ventral view are stereopairs. Scale line 5 mm.

Cinnamon Drab or Orange Buff; ear and uropatagium Hair Brown; wing and radius Fuscous.

Penis (Figure 4)

Long hairs, up to 3 mm on preputium; preputial skin attached to glans at base of head *ca.* 1.5 mm from distal end; head of glans covered by upward projecting narrow tongue of skin from ventral tip of opening; dorsal surface of head of glans with deep median longitudinal groove, ventral surface with slight ventral keel; slight anterolateral elliptical swellings above ventral keel, covered with numerous very small spines, lateral profile an opiculate shape.

Baculum (Figure 5)

Moderately long, greatest length 3.17 ± 0.153 (SD)(N=3), dorsal outline rod shaped shaft with basal one-third gently expanded into a slightly bifurcated base with width 0.73 ± 0.058 (SD)(N=3); evenly bow shaped in lateral profile.

Distribution

West Kimberley district, Western Australia. In tropical woodland (Figure 7c).

Specimens examined

WAM3405.003 (= WAM M3405C) (holotype).

Western Australia: Drysdale R. National Park (14°43′S, 126°54′E) 3 ♀, 1 ♂, WAM4015-8 (paratypes); Mitchell Plateau (14°47′25″S, 125°49′20″E) 1 ♀, WAM21851; Prince Regent R. Reserve (15°31′21″S, 125°12′46″E) 1 ♀, 1 ♂, WAM12250-1 (paratypes); Tunnel Crk (17° 37′S, 125°09′E) 1 ♀, 5 ♂, WAM3405.001(=3405A), WAM3405.002(=3405B), WAM14557-9 (paratypes).

Eptesicus finlaysoni sp. nov.

Figures 4, 5, 7d, 11; Table 1

Holotype

WAM M22407; adult male; body in ethanol, skull separate; liver, heart and kidney removed for electrophoresis, Cossack, Western Australia (20°41′S, 117°11′E) at altitude *ca.* 5 m, from roof of 'Customs House', collected by N.L. McKenzie on 7 August 1984.

Paratypes

See specimens examined.

Diagnosis (mean values)

Eptesicus finlaysoni differs from *E. pumilus*: smaller in most skull, dental and external measurements (Table 1); dorsal inflation of cranium slight or moderate rather than pronounced; rostrum broader as indicated by anteorbital, lacrymal and RC^1-LC^1 widths relative to rostrum length (0.82 v. 0.73, 1.08 v. 0.96, 0.80 v. 0.71, respectively); anterior narial and palatal emarginations usually shallower; anterolateral wing of ectotympanic closer to lateral edge of squamosal; manus digit III with phalanx III shorter relative to phalanx II (0.60 v. 0.87) and phalanx II

longer relative to phalanx I (0.91 v. 0.77); glans penis laterally rather dorsoventrally compressed, urethral opening terminal rather than ventral; baculum longer (3.08 v. 1.6), dorsal outline rod shaped with expanded base rather than arrow shaped, lateral profile more curved.

It differs from *E. caurinus*: metacone-hypocone crista M^1 absent or slight rather than moderate or large; interorbital region generally narrower relative to basicranial length (0.32 v. 0.36); baculum generally longer (v. 2.9).

It differs from *E. douglasorum*: metacone-hypocone crista M^1 absent or slight rather than moderate; hypocone M^{1-2} smaller; manus digit III with phalanx I longer relative to metacarpal (0.38 v. 0.32); skin of face, ears and radius darker.

It differs from *E. darlingtoni*: smaller in most skull, dental and external measurements (Table 1); curve of anterior edge of orbit more even, subcircular; rostrum broader as indicated by anteorbital, lacrymal and RC^1-LC^1 widths relative to rostrum length (v. 0.72, v. 0.96, v. 0.74, respectively); anterior narial emargination usually shallow rather than deep; anterior palatal emargination narrower, usually shallower; manus digit III with phalanx III much shorter relative to phalanx II (v. 0.92) and phalanx II longer relative to phalanx I (v. 0.74); glans penis laterally rather than dorsoventrally compressed, urethral opening terminal rather than ventral; baculum longer (v. 1.7), dorsal outline rod shaped with expanded base rather than blunt arrow shaped, lateral profile more curved.

It differs from *E. troughtoni*: smaller in most skull, dental and external measurements; radius shorter relative to tibia (Figure 10); glans penis more pointed distally, narrower dorsoventrally, urethral opening terminal rather than ventral; baculum generally shorter (v. 3.7), basal notch shorter.

It differs from *E. regulus*: dorsal inflation of cranium slight to pronounced rather than absent; rostrum broader anteriorly as indicated by anteorbital and RC^1-LC^1 widths relative to rostrum length (v. 0.76, v. 0.74, respectively); anterior narial and palatal emarginations narrower, usually shallower; basolateral pterygoid wing present, rather than usually absent; upper tooth row more curved; manus digit III with phalanx III longer relative to phalanx II (v. 0.80) and phalanx II shorter relative to phalanx I and to metacarpal (v. 0.81, 0.35 v. 0.30, respectively); glans penis more pointed distally, much narrower dorsoventrally, lateral urethral lobes absent, urethral opening terminal rather than ventral; baculum generally shorter (v. 3.8), dorsal outline rod shaped with expanded base rather than elongate dart shaped, lateral profile more curved.

It differs from *E. vulturnus*: larger in most skull, dental and external measurements (Table 1); dorsal inflation of cranium slight to pronounced rather than absent or slight; rostrum broader anteriorly as indicated by anteorbital and RC^1-LC^1 widths relative to rostrum length (v. 0.75, v. 0.75, respectively); anterior narial and palatal emarginations narrower, usually shallower; posterior margin of palate terminates well posterior to anterior edge of sphenorbital sinus; basolateral pterygoid wing present; upper tooth row more curved, manus digit III with phalanx III shorter relative to phalanx II (v. 0.80) and phalanx II longer relative

to phalanx I (v. 0.78); glans penis more pointed distally, narrower dorsoventrally, ventral urethral lobe single rather than bilobed; baculum shorter (v. 4.4), base more inclined ventrally, less deeply notched.

It differs from *E. baverstocki*: larger in most skull, dental and external measurements (Table 1); dorsal inflation of cranium slight to pronounced rather than absent or slight; anterior narial and palatal emarginations narrower; posterior margin of palate terminates well posterior to anterior edge of sphenorbital sinus; basolateral pterygoid wing present; upper tooth row more curved; manus digit III with phalanx III longer relative to phalanx II (v. 0.78) and phalanx II shorter relative to phalanx I and to metacarpal (v. 0.84, v. 0.30, respectively); glans penis distally pointed rather than funnel shaped ventral urethral lobe single rather than bilobed, baculum shorter (v. 4.7), lateral profile more curved, partcularly distal end, base less deeply notched.

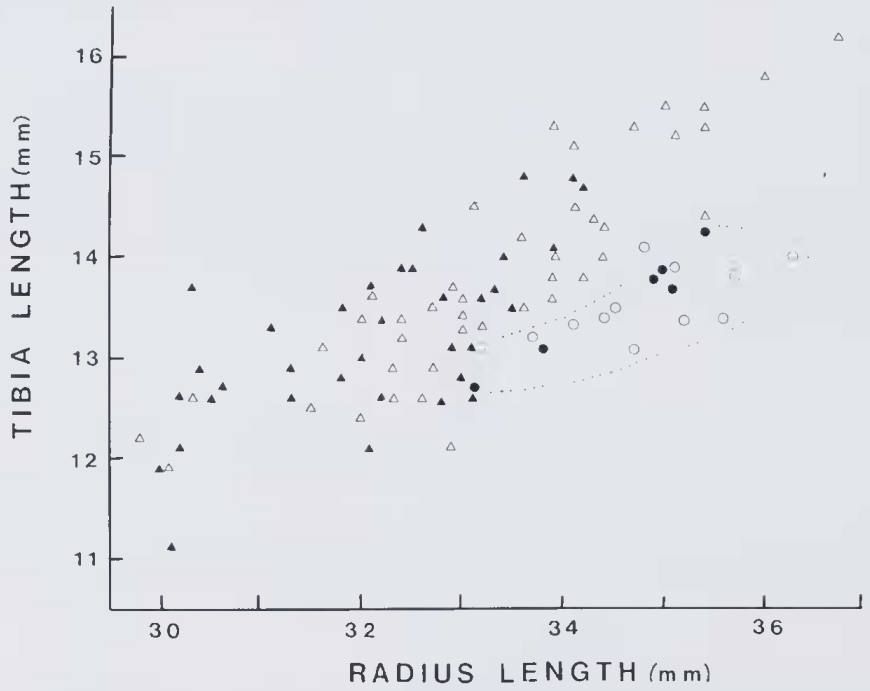


Figure 10 Plot of tibia length against radius length for *Eptesicus finlaysoni* (▲, male; △ female) and *E. troughtoni* (●, male; ○, female).

Description

Skull (Figure 11)

(see also 'General Description of Australian *Eptesicus*'). Greatest skull length moderately long 12.4 (11.3-13.5); cranial inflation varies with region (see Figure 7d for regions): in the Pilbara, Central East and Central West regions most specimens have a moderate inflation (70-85 per cent), some a slight inflation (10-15 per cent)

and some pronounced inflation (4-20 per cent) — in the North West Coastal region equal numbers have slight or moderate inflation and none are pronounced; lambdoidal crest slight to well developed in all regions; anterior narial emargination narrow U to V-shaped, similar in all regions, terminates well anterior to (77-80 per cent) or close to (10-23 per cent) a line joining anterior edges of anteorbital foramina; rostrum short, averages 47.6 per cent of basicranial length; least interorbital distance moderate, averages 32.4 per cent of basicranial length; anteorbital distance moderate, averages 82.0 per cent of rostrum length; inter upper third molar distance moderate, averages 50.5 per cent of basicranial length; lacrymal bar narrow to well developed; postpalatal spine broad to narrow spatulate or triangular, moderately long to long; posterior margin of palate terminates well posterior to anterior edge of sphenorbital sinus; basolateral pterygoid wing coverage of foramen rotundum varies with region: in the Pilbara, Central East and Central West regions it is absent (0-5 per cent) or less than one-third (57-85 per cent) or between one to two-thirds (10-35 per cent) or more than two-thirds (0-8 per cent) — in the North West Coast region it is less than one-third (45 per cent) or between one to two-thirds (50 per cent) or greater than two-thirds (5 per cent)

Dentition

Crista linking base of metacone and hypocone similar in all regions: on M^1 absent (70-75 per cent) or slight (15-30 per cent) or moderate (0-5 per cent) and on M^2 absent (69-80 per cent) or slight (20-32 per cent).

Body size

Body length moderate 40.1 (34.3-46.6), longer than tail length 35.2 (30.7-42.0); relative wing measurements as follows: RL moderate 32.8 (29.8-36.7)≥MCIII>> P1>P2>>P3; tibia length moderate 13.6 (11.1-16.2).

Pelage and skin

Dorsal pelage medium dark, brown, with slightly lighter ventral surface. Hair on cheeks, chin, ear, limbs and patagia monocoloured, the rest bicoloured; on top of head and face distal half Olive Brown and base Clove Brown, on neck distal one-third Wood Brown with base Clove Brown; on dorsum and venter *ca.* 5.2 and 4.0 mm long, respectively; dorsal pelage with distal one-quarter Drab or Wood Brown and base Fuscous Black or Chaetura Black, respectively; chest, sides of body and venter with distal one-quarter to one-third Light Drab and base Fuscous Drab; anal region with distal half Light Drab and base Hair Brown or all Light Drab; cheek and chin Olive Brown and Buffy Brown, respectively; on humerus to elbow medium sparse, Light Drab; femur furred half way to knee, Light Drab; ear one-third haired, Olive Brown; uropatagium with proximal three-quarters extremely sparsely haired, Light Drab; plagiopatagium sparsely haired to *ca.* 10 mm from side of body. Skin of lips, ear, radius and patagia Fuscous.

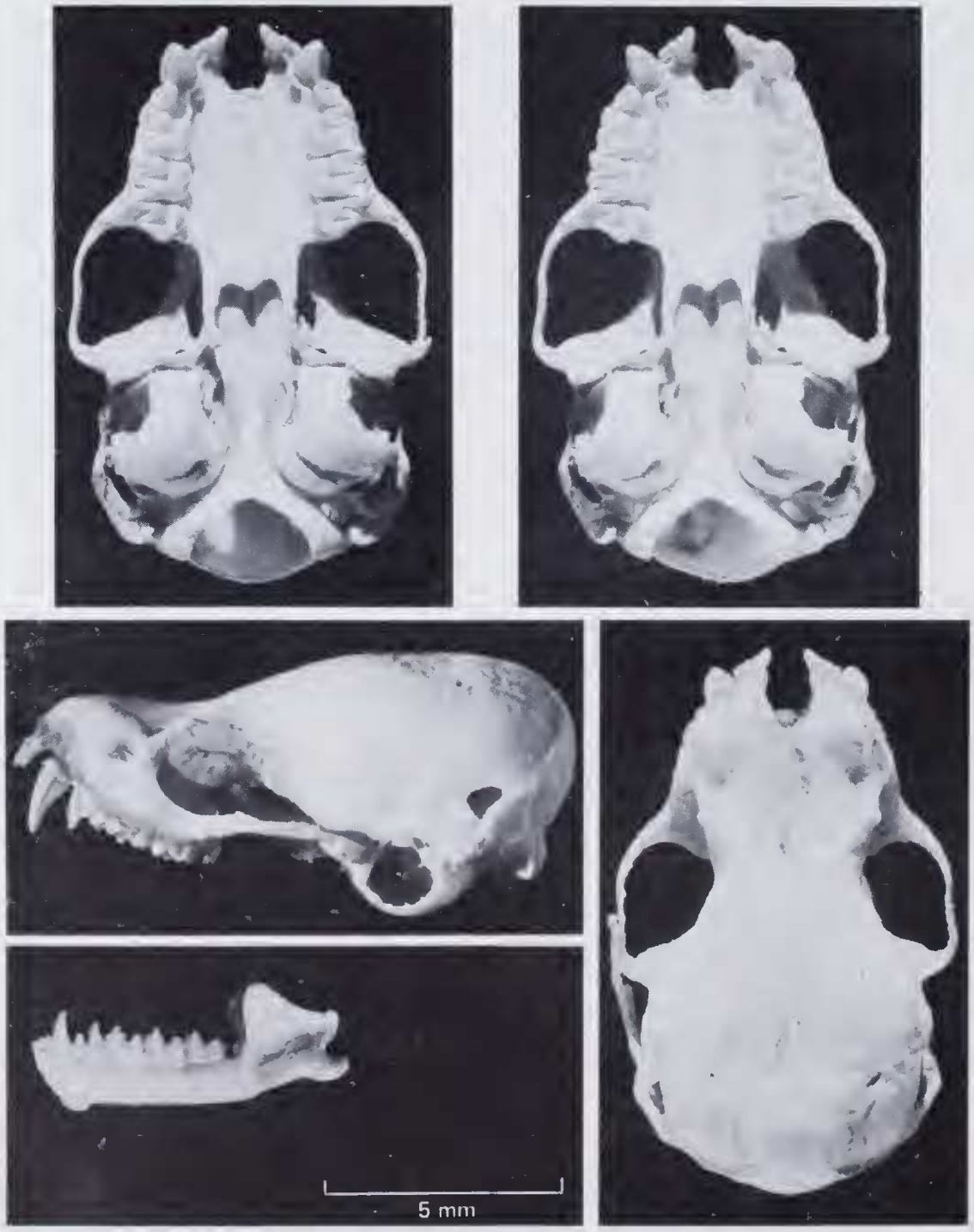


Figure 11 Skull and dentary of *Eptesicus finlaysoni* (WAM M22407, holotype). The ventral view are stereopairs. Scale line 5 mm.

Penis (Figure 4)

Long hairs, up to 3 mm, on preputium; preputial skin attached to glans at base of head *ca.* 1.5 mm from distal end; head of glans laterally compressed; urethral opening at distal end of glans, covered by upward projecting narrow tongue of skin from ventral lip of opening; dorsal surface of head of glans with deep median longitudinal groove – ventral surface with slight ventral keel; slight anterolateral elliptical swellings above ventral keel, covered with numerous very small spines, lateral profile an opiculate shape.

Baculum (Figure 5)

Moderately long, greatest length varies slightly with geographic region: Central East 3.23 ± 0.186 (SD)(N=16), Central West/Pilbara 2.85 ± 0.121 (SD)(N=7) and North West Coastal 3.19 ± 0.146 (SD)(N=8); shaft dorsal outline rod shaped, proximal one-quarter gently expanded into a slightly bifurcated base; basal width varies with region: Central East 0.67 ± 0.103 (SD)(N=6), Central West/Pilbara 0.66 ± 0.098 (SD)(N=7) and North West coastal 0.74 ± 0.92 (SD) (N=8); base and distal end gently curved ventrally, but the base more so.

Distribution

Widely distributed in inland arid parts of Australia: in grasslands and savannahs and shrub communities (Figure 7d).

Etymology

Named after H.H. Finlayson, formerly Curator of Mammals, South Australian Museum. Author of a number of papers on the inland mammals of Australia.

Specimens examined

Paratypes

Central Eastern Region

Northern Territory: Alice Springs area (23°47′S, 133°52′E) 1 ♂, CM5983, (23°54′S, 133° 52′E) 1 ♂, CM2257; Arltunga (23°30′S, 134°37′E) 2 ♀, EBU (B263-4); Katherine (14°28′S, 132°16′E) 1 ♀, 1 ♂, CM1840, CM2123; 50 km SE Roper Bar (*ca.* 15°00′S, 134°50′E) 1 ♂, CM10862; Great Western Mine (19°27′S, 134°03′E) 4 ♂, EBU (B125-7), CM4169; The Granites (20°30′S, 130°21′E) 1 ♂, WAM19010.

Queensland: Cloncurry (20°42′S, 140°30′E) 4 ♀, J6553, J6557-8, J6562; 25 km E Georgetown (18°17′S, 143°46 E) 1 ♂, EBU B74.

South Australia: Arkaroola (31°47′S, 138°30′E) 2 ♀, 1 ♂, EBU B401-3; Brachina Gorge (31°21′S, 138°37′E) 1 ♀, EBU SP106; Mt Gee (*ca.* 30°20′S, 139°22′E) 3 ♀, SAM 9137-9; Oodnadatta (27°37′S, 135°34′E) 1 ♀, EBU B407.

Pilbara Region

Western Australia: Abydos Stn (21°26′00″S, 118°55′40″E) 1 ♂, WAM19323; Cossack (20°41′S, 117°11′E) 2 ♀, WAM (22406, 22408); Gallery Hill (21°40′20″S, 119°02′25″E) 1 ♀, WAM19325; Hammersley Range (22°23′22″S, 118°27′36″E) 1 ♀, 1 ♂ WAM (18689, 18720); Middle Crk (21°52′S, 120°16′E) 3 ♂, WAM (12666, 12668, 12671); Mt Meharry (23°12′00″S, 118°49′30″E) 1 ♀, WAM16830; Opthalmia Range (23°16′50″S, 119°11′20″E) 1 ♂, WAM 19505; Paraburdoo (23°13′30″S, 117°37′00″E) 1 ♀, WAM14940; Shay Gap (20°31′S, 120° 08′E) 1 ♀, 4 ♂, WAM (16779, 16791-3, 16795); Yandicoogina Crk (22°47′10″S, 119°15′00″E) 1 ♀, WAM 18987.

NW Coastal Region

Western Australia: Cape Range (21°51′00″S, 114°06′30″E) 7 ♀, 2 ♂, WAM 19375-84; Carrarang HS. (26°22′50″S, 113°18′50″E) 1 ♀, WAM8749; Dirk Hartog Island (25°57′00″S, 113°09′45″E) 3 ♀, 1 ♂, WAM 10620-3, (25°43′15″S, 113°03′25″E) 1 ♂, WAM11915; Vlaming Head (21°48′30″S, 114°06′40″E) 1 ♀, 2 ♂, WAM (5042, 8723, 8726); 7.5 km NE Yardie HS. (21°51′05″S, 114°04′20″E) 2 ♀, 4 ♂, WAM (5147, 14562, 20933-6).

Central Western Region

Western Australia: Ankatell Ridge (20°37′20″S, 122°42′10″E) 1 ♂, WAM22819, (20°23′00″S, 122°06′50″E) 1 ♀, WAM22822; Bluff Point (28°08′S, 124°13′E) 1 ♂, WAM14619; Canning Stock Route (23°45′S, 122°31′E) 1 ♀, 1 ♂, WAM 14996-7; Charlies Knob (25°03′S, 125°00′E) 1 ♀, WAM14625; Dandaraga Stn (28°07′40″S, 119°40′20″E) 1 ♀, WAM18730; Durba Spring (23°45′20″S, 122°31′00″E) 3 ♀, WAM 14407-9; Edgar Range (18°25′10″S, 123°05′30″E) 1 ♂, WAM15059; Ghanda Rockhole (26°36′10″S, 125°51′30″E) 1 ♂, WAM 13375; Godfrey's Tank (20°15′S, 126°34′E) 1 ♂, WAM22823; Great Sandy Desert (22°50′S, 122°01′E) 1 ♀, 1 ♂, WAM (22814, 22816); Logue River (17°40′30″S, 123°22′30″E) 1 ♀, 1 ♂, WAM (19345, 19361); Miss Gibson Hill (26°52′S, 126°22′E) 1 ♀, 2 ♂, WAM (13333, 13335-6); Mt Anderson (18°02′00″S, 123°53′30″E) 1 ♀, 1 ♂, WAM 19335-6; Mt Charles (25°45′S, 126°11′E) 1 ♂, WAM14626; Mt Wardiacco (28°59′00″S, 118°13′20″E) 1 ♀, WAM13475.001; Mullewa (28°06′S, 115°42′E) 1 ♂, WAM15500; Peak Hill (25°38′S, 118°43′E) 1 ♂, WAM 12986; Wiluna Stn (26°36′00″S, 120°15′09″E) 2 ♂, WAM19106, CM4794.

Eptesicus darlingtoni Allen, 1933

Figures 4, 5, 7e, 12; Table 1

Eptesicus darlingtoni Allen, 1933: J. Mammal. 14: 150-151.

Eptesicus sagittula McKean, Richards and Price, 1978: *Aust. J. Zool.* 26: 529-537; 13 km NW Braidwood, New South Wales.

Holotype

Museum of Comparative Zoology No. 29113; adult female; skin and skull separate; Macpherson Ranges, Queensland, altitude *ca.* 915 m; collected by Dr Philip J. Darlington on 10 March 1932.

Diagnosis (mean values)

Eptesicus darlingtoni differs from *E. pumilus*: larger in all skull, dental and external measurements (Table 1); dorsal inflation of cranium slight or moderate rather than pronounced; anterior narial emargination deep rather than shallow; anterior palatal emargination generally deep rather than shallow; sphenorbital sinus with anterolateral margin convex rather than concave; anterolateral wing of ectotympanic closer to lateral edge of squamosal; manus digit III with phalanx III longer relative to phalanx II (0.92 v. 0.87); baculum dorsal outline similar, but distal end pointed rather than square, base more inclined ventrally.

It differs from *E. caurinus*: much larger in all skull, dental and external measurements (Table 1); anterior narial emargination deep rather than shallow; anterior palatal emargination shallower; curve of anterior edge of orbit oval rather than subcircular; rostrum narrower as indicated by anteorbital, lacrymal and RC^1-LC^1

widths relative to rostrum length (0.72 v. 0.84, 0.96 v. 1.07, 0.74 v. 0.80, respectively); metacone-hypocone crista M^1 absent or slight rather than moderate or large; hypocone M^{1-2} smaller; manus digit III with phalanx III much longer relative to phalanx II (v. 0.55) and phalanx II shorter relative to phalanx I (0.74 v. 0.95); glans penis dorsoventrally rather than laterally compressed, urethral opening ventral rather than terminal; baculum shorter (1.7 v. 2.9), dorsal outline blunt arrow shaped rather than rod shaped with expanded base, lateral profile less curved.

It differs from *E. douglasorum*: dorsal inflation of cranium slight or moderate rather than moderate or pronounced; anterior narial and palatal emarginations deep rather than shallow; curve of anterior edge of orbit oval rather than subcircular; metacone-hypocone crista M^1 absent or slight rather than moderate; hypocone M^{1-2} larger; manus digit III with phalanx III much longer relative to phalanx II (v. 0.54) and phalanx II much shorter relative to phalanx I (v. 1.04); skin of face, ears and radius darker; glans penis dorsoventrally rather than laterally compressed, urethral opening ventral rather than terminal; baculum much longer (v. 3.2), dorsal outline blunt arrow shaped rather than rod shaped with expanded base, lateral profile essentially flat rather than bow shaped.

It differs from *E finlaysoni*: larger in most skull, dental and external measurements (Table 1); curve of anterior edge of orbit oval rather than subcircular; rostrum narrower as indicated by anteorbital, lacrymal and RC^1-LC^1 widths relative to rostrum length (v. 0.82, v. 1.08, v. 0.80, respectively); anterior narial emargination deep rather than usually shallow; anterior palatal emargination broader, usually deeper; manus digit III with phalanx III much longer relative to phalanx II (v. 0.60) and phalanx II shorter relative to phalanx I (v. 0.91); glans penis dorsoventrally rather than laterally compressed, urethral opening ventral rather than terminal; baculum shorter (v. 3.08), dorsal outline blunt arrow shaped rather than rod shaped with expanded base, lateral profile less curved.

It differs from *E. troughtoni*: larger in most skull, dental and external measurements (Table 1); curve of anterior edge of orbit oval rather than subcircular; rostrum narrower as indicated by anteorbital, lacrymal and RC^1-LC^1 widths relative to rostrum length (v. 0.81, v. 1.06, v. 0.77, respectively); anterior narial emargination deep rather than usually shallow; manus digit III with phalanx III longer relative to phalanx II (v. 0.67) and phalanx II shorter relative to phalanx I (v. 0.87); glans penis dorsoventrally rather than laterally compressed; baculum shorter (v. 3.7), dorsal outline blunt arrow shaped rather than rod shaped with expanded base, lateral profile less curved, base less deeply notched.

It differs from *E. regulus*: larger in most skull, dental and external measurements (Table 1); dorsal inflation of cranium slight or moderate rather than absent or slight; curve of anterior edge of orbit oval rather than subcircular; anterior narial emargination usually narrower, deeper; basolateral pterygoid wing present rather than usually absent; manus digit III with phalanx III longer relative to phalanx II (v. 0.80) and phalanx II shorter relative to phalanx I (v. 0.81); glans

penis much narrower dorsoventrally, lateral urethral folds absent; baculum shorter (v. 3.08), dorsal outline blunt arrow shaped rather than elongate dart shaped.

It differs from *E. vulturnus*: larger in all skull, dental and external measurements (Table 1); dorsal inflation of cranium slight or moderate rather than absent or slight; basolateral pterygoid wing present; curve of anterior edge of orbit oval rather than subcircular; narial emargination deep rather than shallow; posterior margin of palate terminates well posterior to anterior edge of sphenorbital sinus; manus digit III with phalanx III longer relative to phalanx II (v. 0.80); glans penis dorsoventrally compressed rather than bulbous, urethral opening ventral rather than terminal; baculum much shorter (v. 4.4), dorsal outline blunt arrow shaped rather than rod shaped with expanded base, less deeply bifureated, distal tip not inflected ventrally.

It differs from *E. baverstocki*: larger in all skull, dental and external measurements (Table 1); dorsal inflation of cranium slight or moderate rather than absent or slight; curve of anterior edge of orbit oval rather than subcircular; anterior narial emargination deeper, usually narrower; posterior margin of palate well posterior to anterior edge of sphenorbital sinus; basolateral pterygoid wing present; manus digit III with phalanx III longer relative to phalanx II (v. 0.78) and phalanx II shorter relative to phalanx I (v. 0.84); glans penis dorsoventrally compressed rather than funnel shaped; baculum much shorter (v. 4.7), dorsal outline blunt arrow shaped rather than rod shaped with expanded base and slight distal lateral wings, base less deeply notched.

Description

Skull (Figure 12)

(see also 'General Description of Australian *Eptesicus*'). Greatest skull length long 13.4 (12.7-14.1), cranial inflation in mainland specimens (N=19) slight (74 per cent) or moderate (26 per cent) — in small Tasmanian sample (N=7) slight (43 per cent) or moderate (57 per cent); lambdoidal crest slight to moderate; anterior narial emargination generally V-shaped, occasionally narrow U-shaped, terminates close to a line joining the anterior edge of anteorbital foramina; rostrum moderately long, averages 50 per cent of basicranial length; least interorbital distance wide, averages 35.1 per cent of basicranial length; anteorbital distance narrow, averages 71.9 per cent of rostrum length; inter upper third molar distance moderate, averages 50.0 per cent of basicranial length; lacrymal bar moderate to wide; postpalatal spine varies from spinous to broadly spatulate, moderately long; posterior margin of palate terminates well posterior to anterior edge of sphenorbital sinus; basolateral pterygoid wing (in mainland and Tasmanian specimens) covers the foramen rotundum to the following extent: less than one-third (71-79 per cent) or between one to two-thirds (21-29 per cent).

Dentition

Crista linking base of metacone and hypocone (in mainland and Tasmanian specimens) on M^1 absent (71-79 per cent) or slight (21-29 per cent) and on M^2

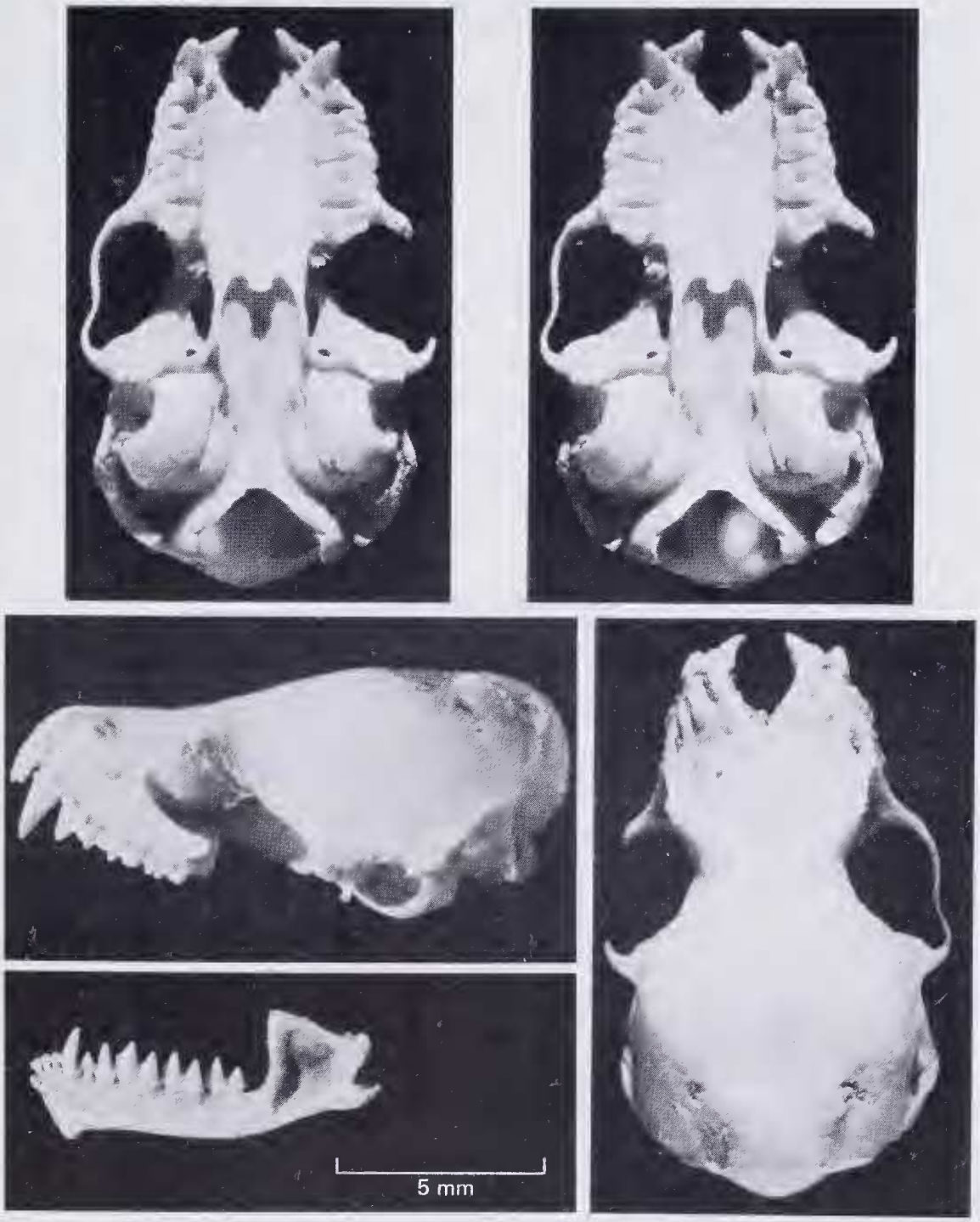


Figure 12 Skull and dentary of *Eptesicus darlingtoni* (J5476, paratype). The ventral view are stereopairs. Scale line 5 mm.

absent (89-100 per cent) or slight (0-11 per cent).

Body size

Body long 44.1 (38.1-48.9), much longer than tail 33.5 (29.2-38.0); relative wing measurements as follows: RL moderate 34.6 (32.5-37.2)>MCIII>>P1>> P2>P3; tibia length small 13.7 (12.3-14.4).

Pelage and skin

Slightly darker pelage on the dorsal than on ventral surface. Hair on head, cheeks, face, dorsum, sides of body and anal region monocoloured, Chestnut Brown; chin, chest, venter, lips and neck Brussels Brown; on humerus and femur sparse, on proximal half only, Buffy Brown; ear furred for one-third the length, Chestnut Brown; uropatagium sparsely furred, Brussels Brown; plagiopatagium sparsely furred *ca.* 5 mm from sides of body; on dorsum *ca.* 5.5 mm long, all Chestnut Brown or distal one-third Olive Brown with base Clove Brown or distal half Buffy Brown with base Fuscous Black; on ventral surface hairs *ca.* 5.2 mm long, all Brussels Brown or distal one-quarter Drab Gray with base Chaetura Black. Skin of lips Brussels Brown and of ear, patagia and radius Fuscous Black.

Penis (Figure 4)

Long hairs, up to 3.3 mm on preputium; preputial skin attached to glans *ca.* 1.0 mm from distal end; glans dorsoventrally compressed dorsal outline obovate shape urethral opening in mid ventral region of head of glans, covered by upward triangular projection of skin from ventral margin of opening; dorsal surface of head of glans with shallow median longitudinal groove; lateral profile of glans a blunt rod shape.

Baculum (Figure 5)

Short, greatest length 1.67 ± 0.047 (SD)(N=11); blunt arrow shaped dorsal outline with base little expanded laterally with width 0.66 ± 0.50 (SD)(N=11); shaft lateral profile straight, base sharply curved ventrally.

Distribution

The Great Dividing Range of eastern Australia south of latitude 28°, Adelaide hills area and Tasmania. Predominantly in sclerophyll forest (Figure 7c).

Specimens examined

Tasmania: Dip Falls (41°00′S, 145°10′E) 1 ♂, EBUE54; Fortescue Forest (43°10′S, 147° 50′E) 2 ♂, EBU (E21, E23); Maracoopa Caves Reserve (41°33′S, 146°15′E) 2 ♂, EBU (E12, E15); near Wet Caves (41°36′S, 146°20′E) 1 ♀, EBUE1; 12 km W Scottsdale (41°20′S, 147° 20′E) 1 ♂, EBUE39.

New South Wales: Acacia Plateau (28°20′S, 152°18′E) 1 ♀, 1 ♂, EBUB344-5; 13 km NW Braidwood (35°21′S, 149°44′E) 1 ♂, CM2290 (holotype *E. sagittula*); Mt Tinderry (35°42′S, 149°16′E) 1 ♀, CM2039; Watagan State Forest (33°00′S, 151°19′E) 3 ♀, EBU (B355-6, 003); Riverlea (35°16′S, 149°53′E) 1 ♀, CM6575; Spirabo State Forest (29°15′S, 152°02′E) 2 ♀, EBUB346-7.

Australian Capital Territory: Canberra (35°17'S, 149°13'E) 1 ♂, CM16022.

South Australia: Big Heath Conservation Park (37°10'S, 140°36'E) 1 ♂, EBUFBH3; Kuitpo Forest (35°09'S, 138°40'E) 1 ♂, EBUB411.

Victoria: Bendigo (36°45'S, 144°15'E) 5 ♀, 2 ♂, EBU (11282/01, 11282/03, 830226/03, 830226/06, 830226/09-11); Koetong (36°09'S, 147°29'E) 1 ♀, C25602.

Queensland: Macpherson Range, (*ca.* 28°12'S, 152°40'E) 1 ♀, J5476 (= MCZ29120 - paratype *E. darlingtoni*).

Lord Howe Island: 4 ♀, 1 ♂, AM2652, AM4741, AM8819 (paratype *E. sagittula*), AM10469, AM11761.

Eptesicus troughtoni sp. nov.

Figures 4, 5, 7f, 13; Table 1

Holotype

JM 5412; adult male; body in ethanol, skull separate; liver, heart, muscle and kidney removed for electrophoresis; from Yarramulla Lava Tunnels, Mt Surprise, Queensland (18°13'30"S, 144°40'30"E), altitude 840 m; collected by Terrance Brian Reardon on 8 August 1982.

Paratypes

See Specimens examined.

Diagnosis (mean values)

Eptesicus troughtoni differs from *E. pumilus*: larger in most skull, dental and external measurements (Table 1); dorsal inflation of cranium moderate rather than pronounced; rostrum broader as indicated by anteorbital, lacrymal and RC^1-LC^1 widths relative to rostrum length (0.81 v. 0.73, 0.77 v. 0.71, 1.06 v. 0.96, respectively); manus digit III with phalanx III shorter relative to phalanx II (0.67 v. 0.87) and phalanx II longer relative to phalanx I (0.87 v. 0.77); glans penis laterally rather than dorsoventrally compressed, urethral opening terminal rather than ventral; baculum longer (3.7 v. 1.6), dorsal outline rod shaped with expanded base rather than arrow shaped, lateral profile more curved, base more deeply notched.

It differs from *E. caurinus*: much larger in all skull, dental and external measurements (Table 1); anterior narial emargination usually broader; hypocone M^{1-2} larger; glans penis less pointed distally, much broader dorsoventrally; baculum longer (v. 2.9), base more deeply notched.

It differs from *E. douglasorum*: anterior narial emargination broader; hypocone M^{1-2} larger; manus digit III with phalanx II shorter relative to phalanx I (v. 1.04) and phalanx I longer relative to metacarpal (0.37 v. 0.32); glans penis less pointed distally, broader dorsoventrally; baculum generally longer (v. 3.2), base less deeply notched, lateral profile less curved.

It differs from *E. finlaysoni*: larger in most skull, dental and external measurements (Table 1); radius longer relative to tibia (Figure 10); glans penis less pointed distally, broader dorsoventrally, urethral opening ventral rather than terminal; baculum generally longer (v. 3.08), base less deeply notched.

It differs from *E. darlingtoni*: smaller in most skull, dental and external measurements (Table 1); curve of anterior edge of orbit subcircular rather than oval; rostrum broader as indicated by anteorbital, lacrymal and RC^1--LC^1 widths relative to rostrum length (v. 0.72, v. 0.96, v. 0.74, respectively); anterior narial emargination usually shallow rather than deep; manus digit III with phalanx III shorter relative to phalanx II (v. 0.54) and phalanx II longer relative to phalanx I (v. 0.74); glans penis laterally rather than dorsoventrally compressed; baculum longer (v. 1.7), dorsal outline rod shaped with expanded base rather than blunt arrow shaped, lateral profile more curved.

It differs from *E. regulus*: dorsal inflation of cranium moderate rather than absent or slight; rostrum broader anteriorly as indicated by anteorbital and RC^1-LC^1 widths relative to rostrum length (v. 0.76, v. 0.74, respectively); anterior narial and palatal emarginations narrower, narial usually shallower; basolateral pterygoid wing present rather than usually absent; upper tooth row more curved; manus digit III with phalanx III shorter relative to phalanx II (v. 0.80); glans penis with urethral lobe ventral rather than terminal, lacks lateral urethral folds; baculum dorsal outline rod shaped with expanded base rather than elongate dart shape, curved rather than flat in lateral profile.

It differs from *E. vulturnus*: larger in most skull, dental and external measurements (Table 1); dorsal inflation of cranium moderate rather than absent or slight; rostrum broader anteriorly as indicated by anteorbital and RC^1-LC^1 widths relative to rostrum length (v. 0.75, v. 0.75, respectively); anterior narial and palatal emarginations usually shallower; posterior margin of palate terminates well posterior to anterior edge of sphenorbital sinus; basolateral pterygoid wing present; upper tooth row more curved; manus digit III with phalanx III shorter relative to phalanx II (v. 0.80); glans penis laterally compressed rather than bulbous, ventral urethral lobe single rather than bilobed; baculum shorter (v. 4.4), base more inclined ventrally, distal tip less curved ventrally.

It differs from *E. baverstocki*: larger in most skull, dental and external measurements (Table 1); dorsal inflation of cranium moderate rather than absent or slight; posterior margin of palate terminates well posterior to anterior edge of sphenorbital sinus; basolateral pterygoid wing present; upper tooth row more curved; metaconehypocone crista M^1 absent to moderate rather than always absent; manus digit III with phalanx III shorter relative to phalanx II (v. 0.78); glans penis laterally compressed rather than funnel shaped; baculum shorter (v. 4.7), base more inclined ventrally, lateral distal wings absent.

Description

Skull (Figure 13)

(see also 'General Description of Australian *Eptesicus*'). Greatest skull length moderately long 12.7 (12.2-13.2); cranial inflation slight (4 per cent) or moderate (96 per cent); lambdoidal crest slight to well developed; anterior narial emargination V or narrow U-shaped, terminates well anterior to a line joining anterior

edge of anteorbital foramina (82 per ccnt) or close to this line (18 per cent); rostrum short, averages 49.1 per cent of basicranial length; least interorbital distance wide, averages 35.2 per cent of basicranial length; inter upper third molar distance wide, averages 52.8 per cent of basicranial length; lacrymal bar narrow or moderate; postpalatal spine broad or narrow spatulate or triangular, short or moderately long; posterior margin of palate terminates well posterior to anterior edge of sphenorbital sinus; basolateral pterygoid wing absent in two specimens (9 per cent) – its coverage of the foramen rotundum to the extent of: less than one-third (69 per cent) or between one to two-thirds (22 per cent).

Dentition

Crista linking base of metacone and hypocone on M^1 absent (26 per cent), slight (43 per cent) or moderate (31 per cent) and on M^2 absent (30 per cent), or slight (61 per cent) or moderate (9 per cent).

Body size

Body length moderate 41.5 (37.5-44.2), longer than tail 35.3 (31.4-37.9); relative wing measurements as follows: RL moderate 34.8 (33.0-36.4)≥MCIII >>P1>P2>>P3; tibia length moderate 13.6 (12.7-14.2).

Pelage and skin

Dorsal pelage moderately dark with paler ventral surface. Hair on top of head has distal half Mummy Brown and base Bister; on cheek and chin Tawny Olive; on face Bister; on neck has distal three-quarters Mummy Brown and base Tawny Olive; on dorsum *ca.* 5.5 mm long with distal half Dresden Brown and base Clove Brown; on chest, venter and sides of body *ca.* 5 mm long with distal one-third Tawny Olive and base Fuscous Black; anal region Tawny Olive; humerus very sparsely haired to elbow, Light Buff; femur furred to two-thirds of length, Light Buff; ear furred on basal one-half, distal half Buffy Brown and base Olive Brown; proximal half of uropatagium extremely sparsely haired, Light Buff; plagiopatagium moderately furred to *ca.* 10 mm from side of body. Skin of lips Fuscous Black and of ear, radius and patagia Clove Brown.

Penis (Figure 4)

Long hairs on preputium; preputial skin attached at immediate base of glans head, *ca.* 1.7 mm from distal end; head of glans laterally compressed; opening of urethra at distal end of glans, covered by upward narrow triangular projection of skin from ventral lip of opening; dorsal surface of head of glans with shallow median longitudinal groove with two slight lateral swellings in the middle region of the head; lateral profile of glans approximately rectangular.

Baculum (Figure 5)

Moderately long, greatest length 3.69 ± 0.154 (SD)(N=11); dorsal outline of shaft rod shaped with moderately wide 0.96 ± 0.069 (SD)(N=11) base, moderately

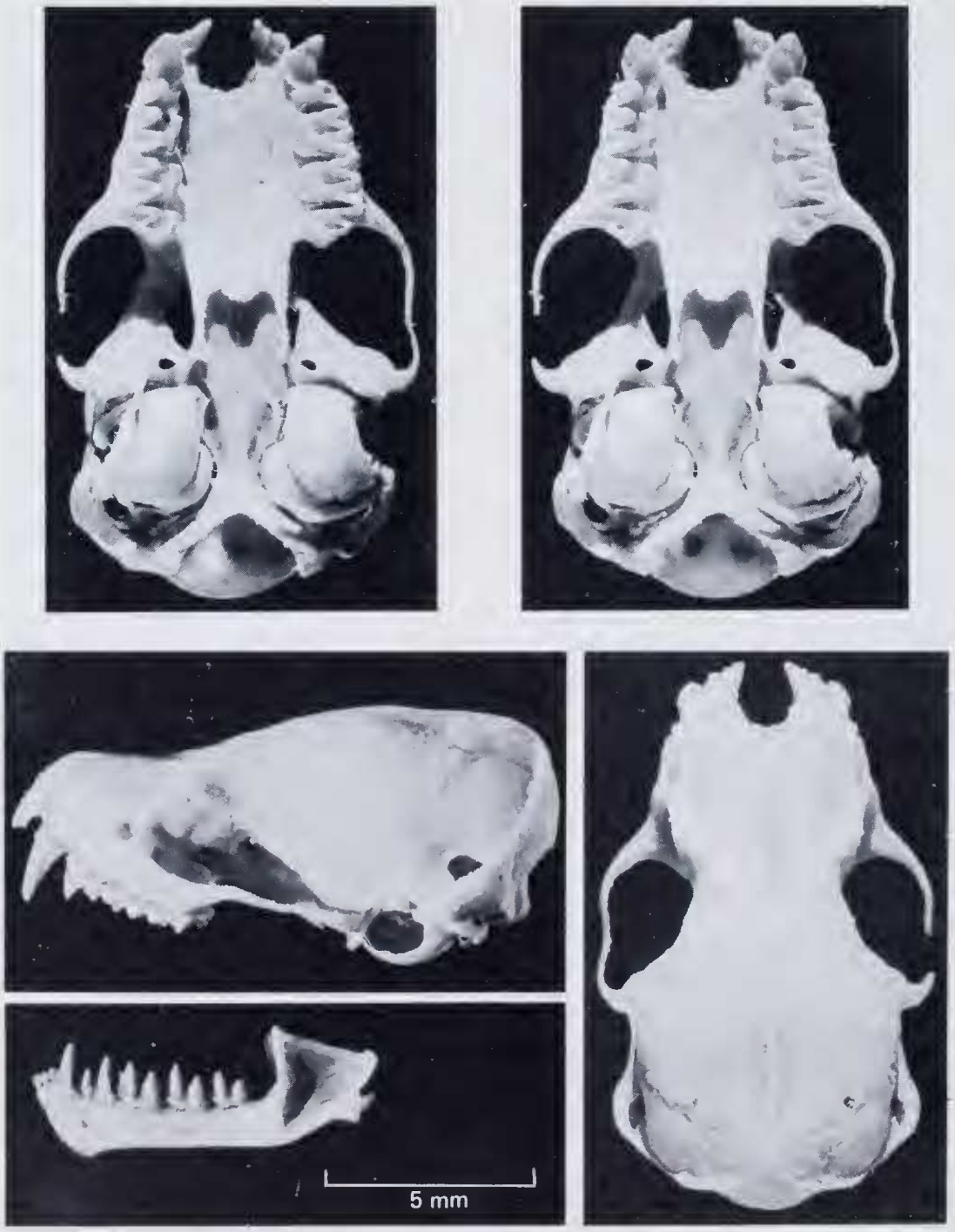


Figure 13 Skull and dentary of *Eptesicus troughtoni* (JM5412, holotype). The ventral view are stereopairs. Scale line 5 mm.

bifurcated; lateral profile bow shaped but with basal one-quarter much more inflected ventrally than distal end.

Distribution

Great Dividing Range of eastern Australia and more coastal country north of latitude 31°S. Predominantly in tropical mixed woodland (Figure 7f).

Etymology

Named after Ellis Le G. Troughton, late Curator of Mammals, the Australian Museum. Author of a number of taxonomic papers on Australian mammals.

Specimens examined

Paratypes

New South Wales: Bonalbo (28°44′S, 152°37′E) 1 ♀, 1 ♂, CM169, CM179; Warrumbungle Range (*ca.* 31°S, 149°E) 2 ♀, 1 ♂, CM2325, CM2330, CM2333.

Queensland: Cape Hillsborough National Park (20°51′S, 145°03′E) 2 ♀, JM759-60; Gin Gin (25°00′S, 151°57′E) 1 ♂, CM5980; Iron Range (12°44′S, 143°17′E) 1 ♀, 1 ♂, CM16005, CM16117; Mt Alford (28°04′S, 152°36′E) 1 ♀, J8830; "Mt Iron Pot", 24 km NE Rockhampton (*ca.* 23°10′S, 150°40′E) 5 ♀, AM10291, AM10294, AM10295, CM16081-2; Mt Molloy (16° 41′S, 145°20′E) 3 ♀, J19036-8; Yarramulla Lava Tunnels (18°13′30″S, 144°40′30″E) 2 ♀, 3 ♂, EBU B61-2, B64-6.

Referred specimens

New South Wales: Bonalbo (28°44′S, 152°37′E) 1 ♂, CM164; Rivertree (28°38′S, 152°18′E) 1 ♂, CM451.

Queensland: Chillagoe (17°09′S, 144°31′E) 1 ♂, CM10843; Iron Range (12°44′S, 143°17′E) 1 ♂, CM6672; "Mt Iron Pot", 24 km NE Rockhampton (*ca.* 23°10′S, 150°40′E) 3 ♂, CM16094, CM16100, CM16102; Ravenswood (20°06′S, 146°53′E) 1 ♂, CM6671; Salvator Rosa National Park (*ca.* 24°50′S, 147°15′E) 1 ♂, CM4384.

Eptesicus regulus (Thomas, 1906)

Figures 4, 5, 7g, 14; Table 1

Pipistrellus regulus Thomas, 1906: Proc. Zool. Soc. (Lond.) p. 470.

Lectotype

BMNH 6.8.1.18, adult, skull only, King River, King George Sound, South Western Australia. Lectotype designated by Hill (1968).

Diagnosis (mean values)

Eptesicus regulus differs from *E. pumilus*: dorsal inflation of cranium absent to moderate rather than pronounced; anterior palatal emargination broader, usually deeper; basolateral pterygoid wing usually absent rather than present; glans penis laterally rather than dorsoventrally compressed, lateral urethral folds present; baculum longer (3.8 v. 1.6), dorsal outline elongate dart shaped rather than arrow shaped.

It differs from *E. caurinus*: larger in most skull, dental and external measurements (Table 1); dorsal inflation of cranium absent to moderate rather than pronounced; rostrum narrower anteriorly as indicated by anteorbital and RC^1-LC^1 widths relative to rostrum length (0.76 v. 0.84, 0.74 v. 0.80, 0.98 v. 1.07, respectively); anterior narial and palatal emarginations deeper, usually broader; basolateral pterygoid wing generally absent rather than present; upper tooth row less curved; metacone-hypocone crista M^1 absent or slight or rarely moderate rather than moderate or large; hypocone M^{1-2} larger; manus digit III with phalanx III longer relative to phalanx II (0.80 v. 0.55) and phalanx II shorter relative to phalanx I (0.87 v. 0.95); glans penis broader dorsoventrally, urethral opening ventral rather than terminal, lateral urethral folds present; baculum longer (v. 2.9), dorsal outline elongate dart shaped rather than rod shaped with expanded base, lateral profile flat rather than curved, base more deeply notched.

It differs from *E. douglasorum*: dorsal inflation of cranium absent to moderate rather than moderate or pronounced, rostrum narrower anteriorly as indicated by anteorbital and RC^1-LC^1 widths relative to rostrum length (v. 0.83, v. 0.79, respectively); anterior narial and palatal emarginations broader, usually deeper; basolateral pterygoid wing usually absent rather than present; upper tooth row less curved; hypocone M^{1-2} larger; metacone-hypocone crista M^{1-2} slight or absent or very rarely moderate rather than moderate only; manus digit III with phalanx III longer relative to phalanx II (v. 0.54) and phalanx II shorter relative to phalanx I (v. 1.04); glans penis less pointed distally, urethral opening ventral rather than terminal, lateral urethral folds present; baculum longer (v. 3.2), dorsal outline elongate dart shaped rather than rod shaped with expanded base, lateral profile flat rather than curved.

It differs from *E. finlaysoni*: dorsal inflation of cranium generally slight rather than generally moderate; rostrum narrower anteriorly as indicated by anteorbital and RC^1-LC^1 widths relative to rostrum length (v. 0.82, v. 0.80, respectively); anterior narial and palatal emarginations broader, usually deeper; basolateral pterygoid wing usually absent rather than present; upper tooth row less curved; manus digit III with phalanx III shorter relative to phalanx II (v. 0.60) and phalanx II longer relative to phalanx I (v. 0.91); glans penis less pointed distally, broader dorsoventrally, urethral opening ventral rather than terminal, lateral urethral folds present; baculum longer (v. 3.1), dorsal outline dart shaped rather than rod shaped with expanded base, lateral profile less curved.

It differs from *E. darlingtoni*: smaller in most skull, dental and external measurements (Table 1); curve of anterior edge of orbit subcircular rather than oval; anterior narial emargination usually broader; basolateral pterygoid wing usually absent rather than present; manus digit III with phalanx III shorter relative to phalanx II (v. 0.92) and phalanx II longer relative to phalanx I (v. 0.74); glans penis broader dorsoventrally, lateral urethral folds present; baculum longer (v. 1.7), dorsal outline elongate dart shaped rather than blunt arrow shaped, base more deeply notched.

It differs from *E. troughtoni*: rostrum narrower anteriorly as indicated by anteorbital and RC^1-LC^1 widths relative to rostrum length (v. 0.81, v. 0.77, respectively); anterior narial and palatal emarginations broader, narial usually deeper; basolateral pterygoid wing usually absent rather than present; upper tooth row less curved; manus digit III with phalanx III longer relative to phalanx II (v. 0.67); glans penis with urethral lobe terminal rather than ventral, lateral urethral folds present; baculum dorsal outline elongate dart shaped rather than rod shaped with expanded base, lateral profile flat rather than curved.

It differs from *E. vulturnus*: larger in most skull, dental and external measurements (Table 1); anterior narial and palatal emarginations usually deeper; posterior margin of palate well posterior to anterior edge of sphenorbital sinus; manus digit III with phalanx I shorter relative to metacarpal (0.37 v. 0.42); glans penis laterally compressed rather than bulbous, urethral opening terminal rather than ventral, lateral urethral folds present; baculum shorter (v. 4.4), dorsal outline elongate dart shaped rather than rod shaped with expanded base, lateral profile essentially flat rather than curved, base less deeply notched, distal end not inclined ventrally.

It differs from *E. baverstocki*: larger in most skull, dental and external measurements (Table 1); anterior narial and palatal emarginations usually deeper; posterior margin of palate generally well posterior to anterior edge of sphenorbital sinus rather than level with it; glans penis with lateral urethral folds rather than funnel shaped; baculum shorter (v. 4.7), dorsal outline elongate dart shaped rather than rod shaped with expanded base and slight distal lateral wings, lateral profile flat rather than curved.

Description

Skull (Figure 14)

(see also 'General Description of Australian *Eptesicus*'). Greatest skull length moderately long 12.7 (11.9-13.4); cranial inflation varies with region: specimens from the forested region of extreme southwestern Western Australia have the most inflated skulls with inflation absent (6 per cent), or slight (69 per cent) or moderate (25 per cent) — those from semi-arid woodland region of southwestern Western Australia and the southeastern mainland regions have cranial inflation absent (44-51 per cent), or slight (41-50 per cent), or moderate (6-8 per cent) — Tasmanian specimens have inflation absent (91 per cent) or slight (9 per cent); lambdoidal crest moderate to well developed; anterior narial emargination U-shaped, terminates well anterior to (50-65 per cent) or close to (35-50 per cent) a line joining anterior edges of anteorbital foramina in the mainland specimens—in the Tasmanian specimens 100 per cent terminated well anterior to this line; rostrum moderately long, averages 50.0 per cent of basicranial length; least interorbital distance narrow, averages 32.4 per cent of basicranial length; anteorbital distance moderate, averages 75.9 per cent of rostrum length; inter upper third molar distance narrow, 48.1 per cent of basicranial length; lacrymal bar usually moderate, occasionally narrow; postpalatal spine variable, spinous to broad spatulate,

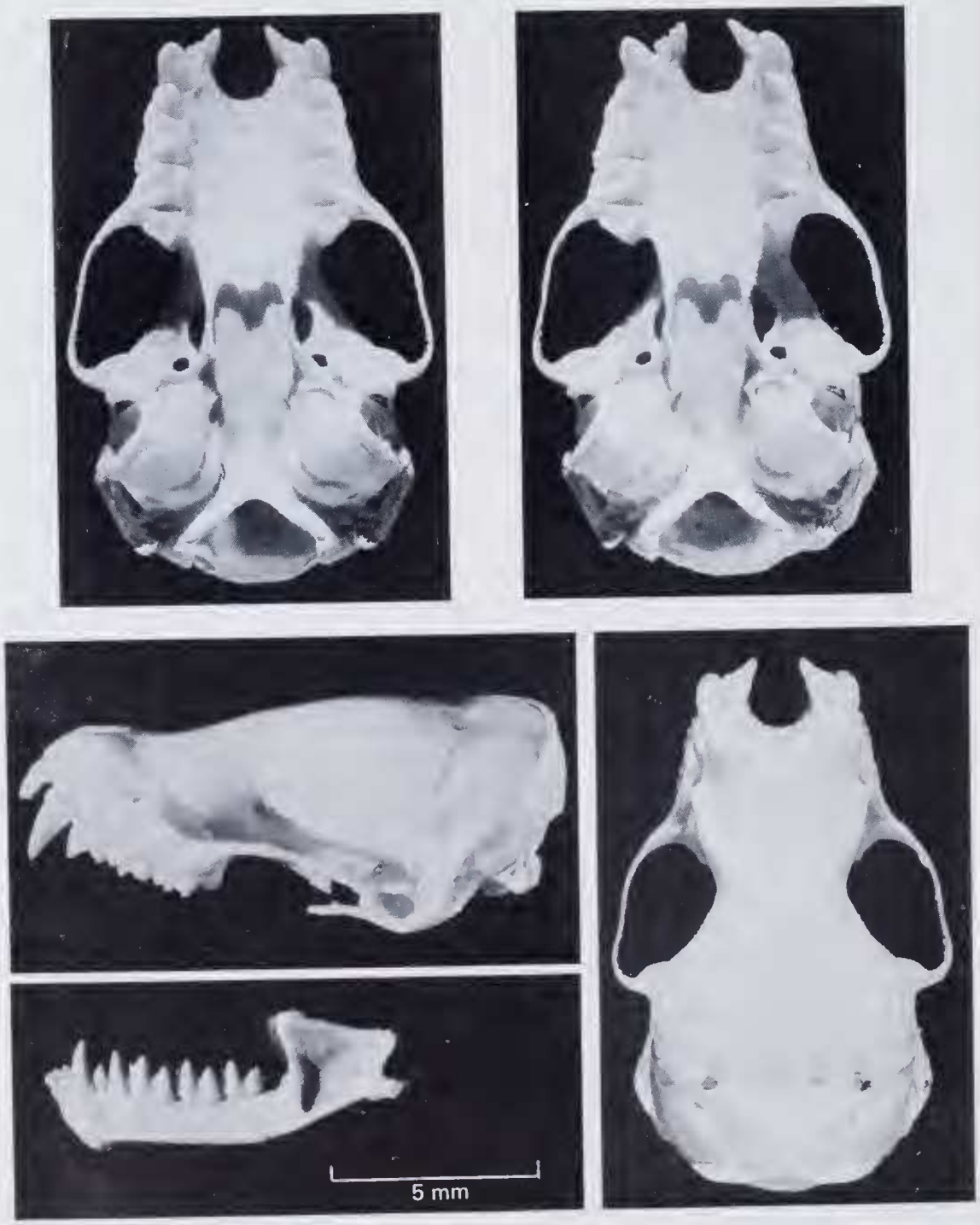


Figure 14 Skull and dentary of *Eptesicus regulus* (WAM M15167). The ventral view are stereo-pairs. Scale line 5 mm.

short to long; posterior margin of palate generally terminates posterior to, or occasionally level with, anterior edge of sphenorbital sinus; in mainland specimens basolateral pterygoid wing generally absent or small and not extending to foramen rotundum (81-87 per cent) or present and covering less than one-third foramen rotundum (13-19 per cent) – absent or very small in Tasmanian specimens.

Dentition

Crista linking base of metacone and hypocone varies with region; in extreme southwestern Western Australia and Tasmania on M^1 absent (27-31 per cent) or slight (56-73 per cent) or moderate (0-13 per cent) and M^2 absent (62-82 per cent) or slight (18-38 per cent) – in the semi-arid southwest and eastern mainland regions on M^1 absent (86-94 per cent) or slight (6-14 per cent) and on M^2 absent (92-94 per cent) or slight (6-8 per cent).

Body size

Body length moderate 41.4 (36.2-46.6), much longer than tail length 31.7 (28.5-39.0); relative wing measurements as follows: RL moderate 31.2 (28.0-34.4) >MCIII>>P1>>P2>>P3; tibia length small 12.7 (11.4-13.9).

Pelage and skin

Dorsal pelage medium dark with paler ventral surface. Hair on cheek, face and chin Wood Brown; anal region Avellaneous; on top of head and dorsum distal one-quarter to one-third Buffy Brown or Bone Brown or with base Clove Brown and Fuscous Black, respectively; on dorsum and venter *ca.* 5.5 and 5.0 mm, respectively; neck, chest and venter have distal one-quarter Avellaneous with base Fuscous Black – side of body has the same colour patterning but the distal Avellaneous is one-half the length of hairs; proximal half of humerus with very sparse hairs, Avellaneous; femur moderately furred to knee, Avellaneous; ear furred to half length, Wood Brown; uropatagium extremely sparsely haired, Avellaneous; plagiopatagium furred to *ca.* 8 mm from sides of body. Skin of lips and ear Olive Brown and of patagia and radius Clove Brown.

Penis (Figure 4)

Moderate length hairs on preputium; preputial skin attached to shaft of glans *ca.* 2.3 mm from distal end of glans; head of glans laterally compressed; urethral opening ventral and approximately centrally located on head of glans, enclosed by a large lateral fold on either side which meet in the mid line for about 0.5 mm forming a partially enclosed urethral groove; secondary lateral folds are located at base of glans head; distal end of glans smooth and round with slightly raised dorsal hump; lateral profile club shaped.

Baculum (Figure 5)

Moderately long 3.8 ± 0.23 (SD)(N=10); dorsal outline elongate dart shaped, base moderately bifurcated, slightly expanded laterally 0.89 ± 0.057 (SD) (N=10) and dorsoventrally; lateral profile reasonably straight with dorsal inflection of distal one-quarter of shaft.

Distribution

Great Dividing Range of eastern Australia south of latitude 29° S and Tasmania (predominantly dry sclerophyll forest); southeastern South Australia (shrubland and low shrub woodland) and southwestern Western Australia (wet and dry sclerophyll forest, mixed temperate woodland and sclerophyll mallee) (Figure 7g).

Specimens examined

BMNH 6.8.1.18 (lectotype).

Tasmania: Dip Falls (41°00′S, 145°19′E) 1 ♂, EBUE53; Fortescue Forest (43°10′S, 147° 50′E) 1 ♀, 1 ♂, EBU (E19-20, E24); Maracoopa Caves Reserve (41°33′S, 146°15′E) 1 ♀, 1 ♂, EBU (E7, E14); Wet Caves (41°36′S, 146°20′E) 1 ♂, EBUE3; Mt Field National Park (42°40′S, 146°30′E) 2 ♂, EBU (E30, E33); 12 km W Scottsdale (41°20′S, 147°20′E) 1 ♀, 1 ♂, EBU (E38, E49).

Eastern Mainland

New South Wales: Emu Plains (33°45′S, 150°41′E) 1 ♂, AM10317; Tenterfield (29°03′S, 152°01′E) 1 ♀, EBUB348.

South Australia: Chauncey's Line (*ca.* 35°13′S, 139°08′E) 1 ♂, SAM11089; Lake Gilles Conservation Park (32°58′S, 136°45′E) 2 ♀, 6 ♂, SAM (M10302, M10305, M10307, M10310-1, M10334, M10339, M10343); 25 km N Morgan (30°50′S, 139°42′E) 1 ♂, EBUE61; Sutherlands (34°10′S, 139°14′E) 1 ♂, SAM9832.

Victoria: Bendigo (36°46′S, 144°17′E) 8 ♀, 2 ♂, EBU (821120/01, 11282/04-6, 11282/10, 830226/01-2, 830226/04-5, 830226/08); Cheshunt (36°47′S, 146°26′E) 1 ♂, C25199; Chetwynd (37°17′S, 141°25′E) 1 ♂, C24872; East Gippsland 2 ♀, 2 ♂, C25898, C25917-8, C25977; Gembrook State Forest (*ca.* 37°58′S, 145°35′E) 4 ♀, 2♂, AM11875-79, C25022; Goulburn R. (36°19′30″S, 145°21′30″E) 1 ♂, C25638; Whitfield (36°46′S, 146°25′E) 1 ♂, C25207; Wingan R. (37°38′S, 149°29′E) 1 ♂, C24912.

Western Australia: Extreme SW region: Busselton (33°39′S, 115°20′E) 1 ♀, WAM24544; Contine Reserve (32°58′30″S, 116°52′30″E) 1 ♂, WAM19307; Donnelly R. (34°19′20″S, 115°57′30″E) 1 ♂, WAM15167; Dumbleyung Lk. (33°20′S, 117°40′E) 1 ♂, WAM19114; Fremantle (32°03′S, 115°44′E) 2 ♂, WAM921, WAM18003; Jarrahdale (32°16′45″S, 116° 05′50″E) 1 ♀, WAM18998; Kalamunda (31°58′10″S, 116°07′30″E) 1 ♂, WAM6321; Mt Dale (32°07′30″S, 116°17′40″E) 1 ♂, WAM19187; Nannup (33°59′15″S, 115°46′00″E) 1 ♂, WAM 19310; Sabina R. (33°39′S, 115°24′E) 1 ♂, WAM8154; Tarin Rock (33°05′30″S, 118°13′00″E) 1 ♀, WAM8220; Walpole (35°10′S, 116°40′E) 1 ♂, WAM14687; Woodlands (33°59′S, 117°29′E) 1 ♀, 1 ♂, WAM942, WAM990.

Western Australia: SW region: Beacon (30°04′S, 117°51′E) 1 ♂, WAM12555; Black Flag Stn (30°34′S, 121°14′E) 1 ♂, WAM20343; Bungalbin Hill (30°14′S, 119°49′E) 1 ♀, WAM17749; Cockleshell Gully (30°08′50″S, 115°07′20″E) 1 ♀, WAM10900; Die Hardy Range (29°57′30″S, 119°26′30″E) 1 ♀, WAM20699; Koorarawalyee Dam (31°15′30″S, 120°01′00″E) 1 ♂, WAM 20139; Lake Cronin (32°22′50″S, 119°45′30″E) 2 ♀, WAM20109, WAM20112; Marda (30°12′ 45″S, 119°16′40″E) 3 ♀, 1 ♂, WAM17729-30, WAM17736, WAM17913; Newman Rocks (32°07′00″S, 123°10′25″E) 1 ♀, WAM16753; Woodline (31°57′S, 122°24′E) 1 ♀, WAM20159, (31°50′S, 122°19′E) 1 ♀, WAM20178, (31°55′S, 122°24′E) 1 ♀, WAM17970.

Eptesicus vulturnus Thomas, 1914

Figures 4, 5, 7h, 15; Table 1

Eptesicus pumilus vulturnus Thomas, 1914: Ann. Mag. Nat. Hist., (8) xiii, p. 440.

Vespertilio pygmaeus Becker, 1858 (not *Vespertilio pygmaeus* Leach, 1825): Trans. Phil. Inst. Vic., III, pp. 38-40, Pl., Oakleigh, Dandenong Ranges, Victoria.

Holotype

BMNH 7.1.1.375, adult female; skin, skull separate; from Tasmania; obtained by Mr Tomes from J.P. Verreaux.

Diagnosis (mean values)

Eptesicus vulturnus differs from *E. pumilus*: dorsal inflation of cranium absent or slight rather than pronounced; anterior palatal emargination broader, usually deeper; postpalatal spine generally larger; posterior margin of palate terminates level with or slightly posterior to the anterior edge of sphenorbital sinus rather than well posterior to it; basolateral pterygoid wing generally absent rather than present; anterolateral wing of ectotympanic closer to lateral edge of squamosal; glans penis bulbous rather than dorsoventrally compressed, urethral opening terminal rather than ventral; baculum longer (4.4 v. 1.6), dorsal outline rod shaped with expanded base rather than arrow shaped, base more deeply notched and distal end more inclined ventrally.

It differs from *E. caurinus*: smaller in most skull and dental measurements (Table 1); dorsal inflation of cranium absent or slight rather than pronounced or moderate; rostrum narrower anteriorly as indicated by anteorbital and RC^1-LC^1 widths relative to rostrum length (0.75 v. 0.84, 0.75 v. 0.80, respectively); anterior narial and palatal emarginations broader, usually deeper; posterior margin of palate terminates level with or slightly posterior to the anterior edge of sphenorbital sinus rather than well posterior to it; basolateral pterygoid wing generally absent rather than present; upper tooth row less curved; hypocone M^{1-2} larger; metacone-hypocone crista M^1 absent or slight rather than moderate or large; manus digit III with phalanx III longer relative to phalanx II (0.80 v. 0.55) and phalanx II shorter relative to phalanx I (0.78 v. 0.95); glans penis distally blunt rather than pointed, bulbous rather than dorsoventrally compressed, ventral urethral lobe with two subcircular winged lobes rather than a single fleshy lobe; baculum longer (v. 2.9), lateral profile less curved, base more deeply notched.

It differs from *E. douglasorum*: smaller in most skull, dental and external measurements (Table 1); dorsal inflation of cranium absent or slight rather than moderate or pronounced; rostrum narrower anteriorly as indicated by anteorbital and RC^1-LC^1 widths relative to rostrum length (v. 0.83, v. 0.79, respectively); anterior palatal emargination broader; posterior margin of palate terminates level with or slightly posterior to the anterior edge of sphenorbital sinus rather than well posterior to it; basolateral pterygoid wing generally absent rather than present; hypocone M^{1-2} larger; metacone-hypocone crista M^1 absent or slight rather than moderate; manus digit III with phalanx III longer relative to phalanx II (v. 0.54) and phalanx II shorter relative to phalanx I (v. 1.04); glans penis distally blunt rather than pointed, bulbous rather than laterally compressed, ventral urethral lobe with two subcircular winged lobes rather than a single fleshy lobe; baculum longer (v. 3.2), base more deeply notched and less inclined ventrally, distal end more inclined ventrally.

It differs from *E. finlaysoni*: smaller in most skull, dental and external measurements (Table 1); dorsal inflation of cranium absent or slight rather than generally moderate; rostrum narrower anteriorly as indicated by anteorbital and RC^1-LC^1 widths relative to rostrum length (v. 0.82, v. 0.80, respectively); anterior narial and palatal emarginations broader, usually deeper; posterior margin of palate terminates level with or slightly posterior to anterior edge of sphenorbital sinus rather than well posterior to it; basolateral pterygoid wing generally absent rather than present; upper tooth row less curved; manus digit III with phalanx III longer relative to phalanx II (v. 0.60) and phalanx II shorter relative to phalanx I (v. 0.91); glans penis distally funnel shaped rather than pointed, ventral urethral lobe with two subcircular winged lobes rather than a single fleshy lobe; baculum longer (v. 3.1), base more deeply notched and less inclined ventrally, distal end more inclined ventrally.

It differs from *E. darlingtoni*: smaller in all skull, dental and external measurements (Table 1); dorsal inflation of cranium absent or slight rather than slight or moderate; curve of anterior edge of orbit subcircular rather than oval; narial emargination shallow rather than deep; posterior margin of palate terminates level with or slightly posterior to the anterior edge of the sphenorbital sinus rather than well posterior to it; basolateral pterygoid wing generally absent rather than present; manus digit III with phalanx III shorter relative to phalanx II (v. 0.92); glans penis bulbous rather than dorsoventrally compressed, urethral opening terminal rather than ventral; baculum longer (v. 1.7), dorsal outline rod shaped with expanded base rather than blunt arrow shaped, base more deeply bifurcated and less inclined ventrally, distal end more inclined ventrally.

It differs from *E. troughtoni*: smaller in most skull, dental and external measurements (Table 1); dorsal inflation of cranium absent or slight rather than moderate; rostrum anteriorly narrower as indicated by anteorbital and RC^1-LC^1 widths relative to rostrum length (v. 0.81, v. 0.77, respectively); anterior narial and palatal emarginations usually deeper; posterior margin of palate terminates level with or slightly posterior to the anterior edge of sphenorbital sinus rather than well posterior to it; basolateral pterygoid wing generally absent rather than present; upper tooth row less curved; manus digit III with phalanx III longer relative to phalanx II (v. 0.67); glans penis bulbous rather than laterally compressed, ventral urethral lobe with two subcircular winged lobes rather than a single fleshy lobe; baculum longer (v. 3.7), base less inclined ventrally, distal end more inclined ventrally.

It differs from *E. regulus*: smaller in most skull, dental and external measurements (Table 1); anterior narial and palatal emarginations usually shallower; posterior margin of palate terminates level with or slightly posterior to anterior edge of sphenorbital sinus rather than well posterior to it; manus digit III with phalanx I longer relative to metacarpal (0.42 v. 0.37); glans penis bulbous rather than laterally compressed, urethral opening ventral rather than terminal, lateral urethral folds absent; baculum longer (v. 3.8), dorsal outline rod shaped with

expanded base rather than elongate dart shaped, lateral profile curved rather than flat, distal end much more inclined ventrally.

It differs from *E. baverstocki*: metacone-hypocone crista M^1 absent or slight rather than always absent; manus digit III with phalanx I longer relative to metacarpal (v. 0.36); glans penis bulbous rather than funnel shaped, urethral opening terminal rather than ventral; baculum base narrower and more deeply notched, distal end without slight lateral wings.

Description

Skull (Figure 15)

(see also 'General Description of Australian *Eptesicus*'). Greatest skull length moderately long 12.2 (11.8-12.7); cranial inflation similar in mainland and Tasmanian specimens, absent (25-30 per cent) or slightly inflated (70-75 per cent); lamboidal crest slight to moderate; anterior narial emargination variable, narrow or broad U-shaped or V-shaped, in mainland and Tasmanian specimens terminates well anterior to a line joining anterior edges of anteorbital foramina (91-100 per cent) or close to this line in 9 per cent of mainland specimens; rostrum length moderate, averages 49.5 per cent of basicranial length; least interorbital distance moderate, averages 33.0 per cent of basicranial length; anteorbital distance moderate, averages 74.5 per cent of rostrum length; inter upper third molar distance moderate, averages 49.5 per cent of basicranial length; lacrymal bar usually moderate, occasionally narrow; postpalatal spine narrow or broadly spatulate, or triangular shaped; posterior margin of palate terminates level with or just posterior to anterior edge of sphenorbital sinus; basolateral pterygoid wing generally absent (91 per cent) but in 9 per cent of specimens present and covers less than one-third of foramen.

Dentition

Crista linking base of metacone and hypocone on M^1 absent (48 per cent) or slight (52 per cent) and M^2 absent (83 per cent) or slight (17 per cent).

Body size

Body length moderate 40.2 (34.7-48.0), much longer than tail 30.0 (26.5-33.8); relative wing measurements as follows: RL small 28.4 (26.3-32.8) $\geqslant$ MCIII>>P1>>P2>P3; tibia length small 12.0 (11.2-12.7).

Pelage and skin

Dorsal pelage dark with slightly paler ventral surface. Hair bicoloured except those on cheek, face, chin, ear, limbs, patagia, femur and anal region (Buffy Brown); on top of head with distal one-third Bone Brown and basal part Fuscous Black; neck with distal one-third Buffy Brown and base Fuscous Black; on dorsum *ca.* 5 mm long with distal one-quarter Fuscous or Buffy Brown and base Fuscous Black; on chest and venter *ca.* 5.5 mm long with distal one-quarter Buffy Brown and base Fuscous Black; side of body with distal one-third Buffy Brown and base

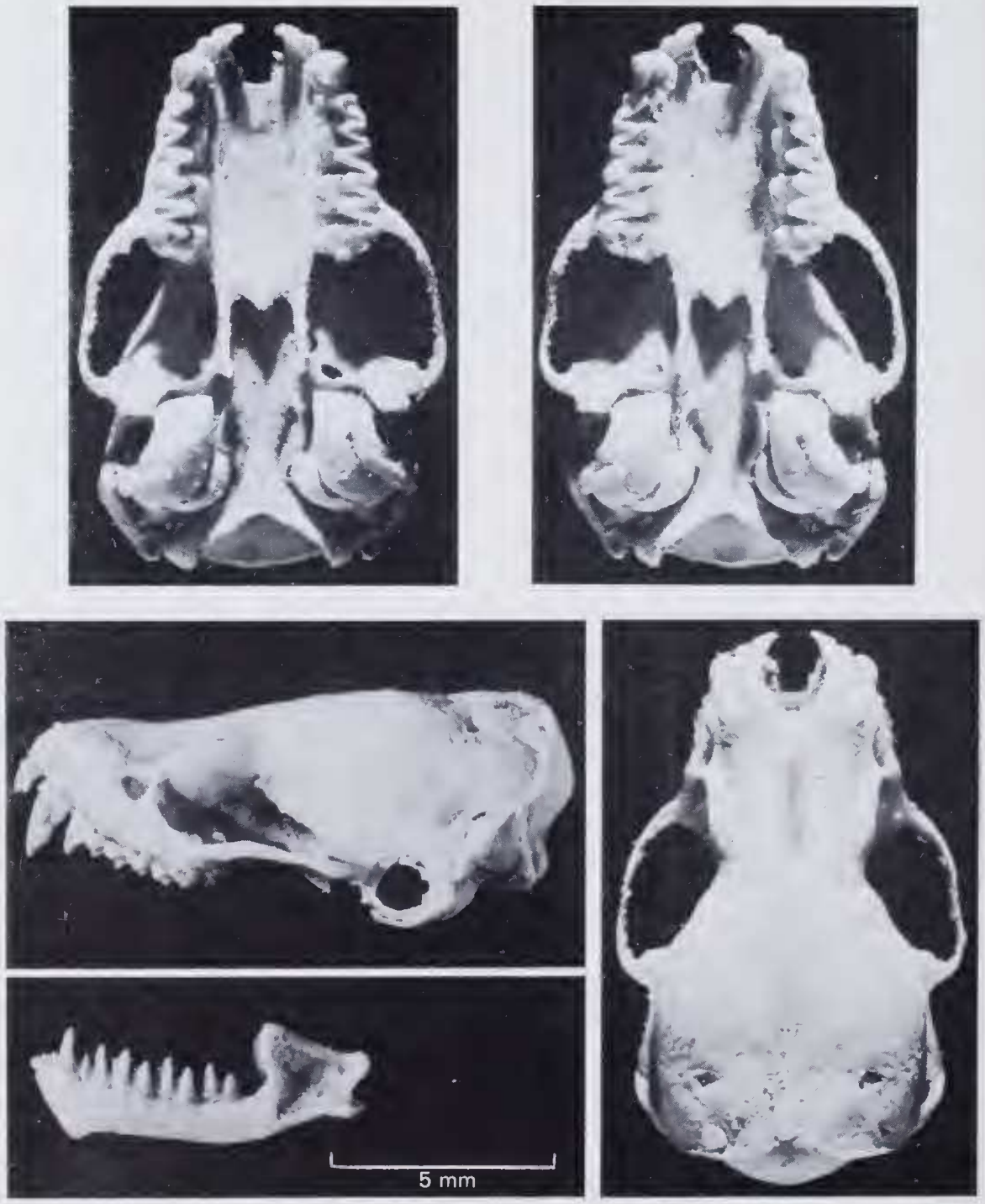


Figure 15 Skull and dentary of *Eptesicus vulturnus* (EBU E34). The ventral view are stereo-pairs. Scale line 5 mm.

Fuscous Black; humerus with very sparse hairs on proximal half, Buffy Brown; femur with extremely sparse hairs half-way to knee, Light Drab; ear with basal one-third haired, Bone Brown; uropatagium covered with extremely sparse hairs, Light Drab; plagiopatagium with very sparse hairs to 5 mm from side of body, Buffy Brown. Skin of lips Olive Brown; ear Clove Brown; radius and patagia Fuscous Black or Buffy Brown.

Penis (Figure 4)

Short hairs 1.5 mm long on preputium; attachment of preputial skin to glans shaft behind head *ca.* 2.3 mm from distal end; glans club shaped; urethral opening at anteroventral aspect of glans, opening covered by a spatulate lobe rising from either side of the mid ventral edge of this opening; dorsal and ventral surface of head with shallow median longitudinal groove.

Baculum (Figure 5)

Long 4.39 ± 0.129 (SD)(N=10), dorsal outline a rod shaped shaft with moderately expanded base 0.87 ± 0.048 (SD)(N=10), deeply bifurcated to 25 per cent greatest length; in lateral profile base little deflected ventrally, distal 10 per cent sharply deflected ventrally.

Distribution

The Great Dividing Range of eastern Australia and associated escarpments south of latitude 30°S and Tasmania. In temperate mixed woodland and wet and dry schlerophyll forest (Figure 7h).

Specimens examined

BMNH 7.1.1.375 (holotype).

Tasmania: Maracoopa Caves Reserve (41°33′S, 146°15′E) 2 ♂, EBU (E6, E13); Mt Field National Park (42°40′S, 146°30′E) 2 ♂, EBU (E31, E34); Risdon Vale (42°50′S, 147°20′E) 1 ♀, 1 ♂, EBUE17-8; 12 km W Scottsdale (41°20′S, 147°20′E) 1 ♀, 2 ♂, EBU (E42, E50-1).

New South Wales: Armidale (30°54′S, 151°08′E) 1 ♀, AM10604; Bulahdelah (32°25′S, 152°12′E) 1 ♀, AM7191; Cooranbong (33°05′S, 151°27′E) 1 ♀, AM11460; Glenbrook (33°46′S, 150°37′E) 1 ♂, AM5265; Griffith (34°17′S, 146°03′E) 3 ♂, AM11796-8; Mumbulla State Forest (36°33′S, 149°52′E) 1 ♂, AM12772; Muswellbrook (32°16′S, 150°54′E) 3 ♀, 1 ♂, AM11164-67; Pilliga (30°21′S, 148°53′E) 2 ♀, 1 ♂, AM12522-4; 13 km W Coonabarrabran (31°16′S, 149°10′E) 2 ♂, AM10314, EBUB360; Willandra National Park (33°29′S, 145°32′E) 1 ♀, AM10822.

Australian Capital Territory: Canberra (35°17′S, 149°13′E) 1 ♂, CM10030.

South Australia: Big Heath Conservation Park (37°10′S, 140°36′E) 1 ♀, EBUFBH5.

Victoria: Gembrook State Forest: (*ca.* 37°58′S, 145°35′E) 4 ♂, AM11869-71, AM11874.

Eptesicus baverstocki sp. nov.

Figures 4, 5, 7i, 16; Table 1

Holotype

WAM M17812; adult male; body in ethanol, skull separate, baculum removed (broken); from Yuinmery area, Western Australian Goldfields (28°28′30″S, 119°17′15″E) at altitude *ca.* 450 m; shot by R.A. How on 17 February 1980.

Paratypes

See Specimens examined.

Diagnosis (mean values)

Eptesicus baverstocki differs from *E. pumilus*: dorsal inflation of cranium slight or absent rather than pronounced; anterior palatal emargination broader; post-palatal spine generally larger; posterior margin of palate terminates level with or slightly posterior to anterior edge of sphenorbital sinus rather than well posterior to it; basolateral pterygoid wing absent; anterolateral wing of ectotympanic closer to lateral edge of squamosal; manus digit III with phalanx III shorter relative to phalanx II (0.78 v. 0.87) and phalanx II longer relative to phalanx I (0.84 v. 0.77); glans penis funnel shaped rather than dorsoventrally compressed, ventral urethral lobe bilobed rather than arrow shaped; baculum longer (4.7 v. 1.6), dorsal outline rod shaped with slight lateral distal flanges and expanded base rather than arrow shaped.

It differs from *E. caurinus*: larger in most skull and dental measurements (Table 1); dorsal inflation of cranium absent or slight rather than moderate or pronounced; rostrum narrower anteriorly as indicated by anteorbital and RC^1-LC^1 widths relative to rostrum length (0.76 v. 0.84, 0.78 v. 0.80, respectively); anterior narial and palatal emarginations broader and deeper; posterior margin of palate terminates level with or slightly posterior to anterior edge of sphenorbital sinus rather than well posterior to it; basolateral pterygoid wing absent; upper tooth row usually less curved; hypocone M^{1-2} larger; metacone-hypocone crista M^1 absent rather than moderate or large; manus digit III with phalanx III longer relative to phalanx II (v. 0.55) and phalanx II shorter relative to phalanx I (v. 0.95); glans penis distally funnel shaped rather than pointed, ventral urethral lobe bilobed rather than single; baculum longer (v. 2.0), lateral profile less curved, base less inclined ventrally and base deeply notched, distal end with slight lateral wings.

It differs from *E. douglasorum*: smaller in most skull, dental and external measurements (Table 1); dorsal inflation of cranium absent or slight rather than moderate or pronounced; anterior palatal emargination narrower; posterior margin of palate terminates level with or slightly posterior to anterior edge of sphenorbital sinus rather than well posterior to it; basolateral pterygoid wing absent; hypocone M^{1-2} larger; metacone-hypocone crista M^1 absent rather than moderate; manus digit III with phalanx III longer relative to phalanx II (v. 0.54) and phalanx II shorter relative to phalanx I (v. 1.04); glans penis funnel shaped rather than pointed distally, ventral urethral lobe bilobed rather than single; baculum longer (v. 3.2), lateral profile less curved, base more deeply notched, distal end with slight lateral wings.

It differs from *E. finlaysoni*: smaller in most skull, dental and external measurements (Table 1); dorsal inflation of cranium absent or slight rather than slight to pronounced; anterior narial and palatal emarginations broader; posterior margin of palate terminates level with or slightly posterior to anterior edge of sphenorbital

sinus rather than well posterior to it; basolateral pterygoid wing absent; upper tooth row less curved; manus digit III with phalanx III longer relative to phalanx II (v. 0.54) and phalanx II shorter relative to phalanx I (v. 0.91); glans penis distally funnel shaped, ventral urethral lobe bilobed rather than single; baculum longer (v. 3.1), lateral profile less curved, base more deeply notched, distal end with slight lateral wings.

It differs from *E. darlingtoni*: smaller in all skull, dental and external measurements (Table 1); dorsal inflation of cranium absent or slight rather than slight or moderate; curve of anterior edge of orbit subcircular rather than oval; anterior narial emargination shallower, usually broader; posterior margin of palate terminates level with or slightly posterior to anterior edge of sphenorbital sinus rather than well posterior to it; basolateral pterygoid wing absent; manus digit III with phalanx III shorter relative to phalanx II (v. 0.92) and phalanx II longer relative to phalanx I (v. 0.74); glans penis funnel shaped rather than dorsoventrally compressed; baculum much longer (v. 1.7), dorsal outline rod shaped with expanded base and slight lateral distal wings rather than blunt arrow shaped.

It differs from *E. troughtoni*: smaller in most skull, dental and external measurements (Table 1); dorsal inflation of cranium absent or slight rather than moderate; basolateral pterygoid wing absent; posterior margin of palate terminates level with or slightly posterior to anterior edge of sphenorbital sinus rather than well posterior to it; upper tooth row less curved; manus digit III with phalanx III longer relative to phalanx II (v. 0.67); glans penis funnel shaped rather than laterally compressed; baculum shorter (v. 3.7), base less inclined ventrally.

It differs from *E. regulus*: smaller in most skull, dental and external measurements (Table 1); anterior narial and palatal emarginations usually shallower; posterior margin of palate terminates level with or slightly posterior to anterior edge of sphenorbital sinus rather than generally well posterior to it; glans penis with lateral urethral folds absent; baculum longer (v. 3.8), dorsal outline rod shaped with expanded base rather than elongate dart shaped, lateral profile curved rather than flat.

It differs from *E. vulturnus*: metacone-hypocone crista M^1 always absent rather than absent or slight; manus digit III with phalanx I shorter relative to metacarpal (0.36 v. 0.42); glans penis funnel shaped rather than bulbous, urethral opening ventral rather than terminal; baculum with wider less deeply notched base, distal end less inclined ventrally.

Description

Skull (Figure 16)

(see also 'General Description of Australian *Eptesicus*'). Greatest skull length moderately long 12.1 (11.6-12.5); cranial inflation absent (63 per cent) or slight (37 per cent); lambdoidal crest weak; anterior narial emargination usually narrow U-shape, occasionally broad U-shaped, terminates well anterior to (58 per cent) or close to (42 per cent) a line joining anterior edges of anteorbital foramina;

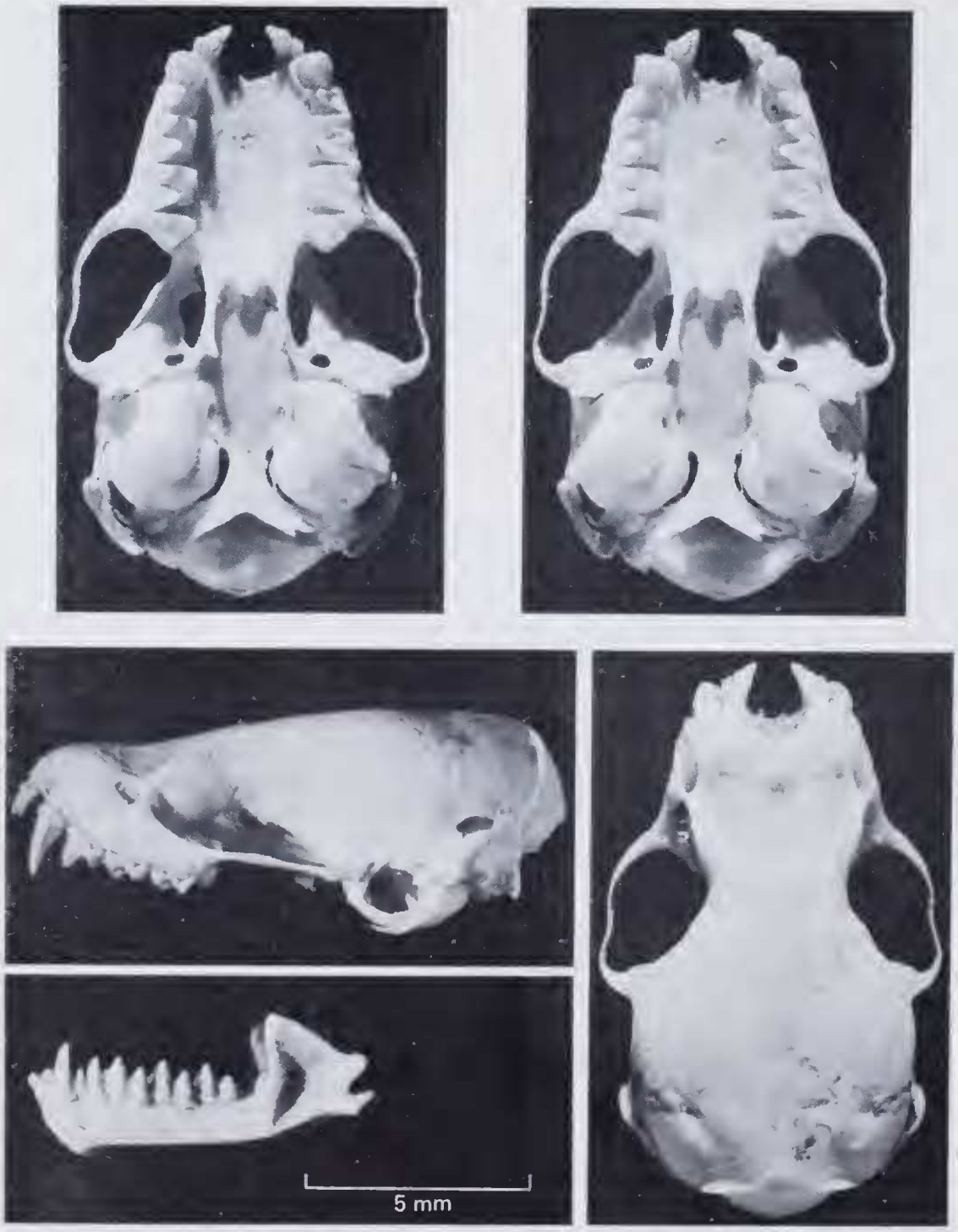


Figure 16 Skull and dentary of *Eptesicus baverstocki* (WAM M17812, holotype). The ventral view are stereopairs. Scale line 5 mm.

rostrum short, averages 48.5 per cent of basicranial length; least interorbital distance narrow, averages 31.1 per cent of basicranial length; anteorbital distance moderately wide, averages 76.0 per cent of rostrum length; inter upper third molar distance narrow, averages 48.5 per cent of basicranial length; lacrymal bar narrow or moderately wide; postpalatal spine narrow spatulate, moderately long; posterior margin of palate terminates level with or slightly posterior to anterior edge of sphenorbital sinus; basolateral pterygoid wing absent or very small, not extending to foramen rotundum.

Dentition

Crista linking base of metacone and hypocone on M^{1-2} absent.

Body size

Body length moderate 40.0 (36.0-43.5), much longer than tail 30.0 (26.5-33.8); relative wing measurements as follows: RL small 28.8 (26.7-31.4)≥MCIII >>P1>>P2>>P3; tibia length small 11.8 (10.8-13.0).

Pelage and skin

Dorsal pelage moderately pale with pale ventral surface. Hair on top of head has distal half Drab and base Fuscous Black; on cheek Pale Smoke Gray; on face and chin Light Drab; on neck has distal one-third Drab Gray and base Fuscous Black; on dorsum between *ca.* 5.3-7.0 mm long, distal half Drab or Olive Brown and base Fuscous Black or Chaetura Black; on chest, venter (*ca.* 4.0 mm long) and side of body distal one-third Drab Gray and base Fuscous Black; anal region Drab Gray; humerus sparsely haired to elbow, Drab Gray; femur furred half way to knee, Drab Gray; ear haired to one-quarter length, Drab Gray; uropatagium very sparsely haired over much of area, Drab Gray; plagiopatagium very sparsely haired to 5 mm from side of body. Skin of lips Brussels Brown; ears and patagia Fuscous and radius Bister.

Penis (Figure 4)

Short hairs on preputium *ca.* 1.7 mm long; preputial skin attached to glans shaft *ca.* 2.3 mm from distal end of glans; glans head funnel shaped with moderately elevated median longitudinal ridge from distal tip to base of shaft, a low translucent semicircular lobe of skin projects from either side of the mid ventral distal rim of the funnel of the glans.

Baculum (Figure 5)

Longest *Eptesicus* baculum: 4.71 ± 0.183 (SD)(N=9); dorsal profile slightly arrow shaped with slight lateral distal wings, base wide 1.02 ± 0.083 (SD)(N=9) and moderately deeply bifurcated; in lateral profile base slightly expanded dorsoventrally, shaft narrowing distally and gently arched ventrally.

Distribution

Widely distributed in inland arid parts of Australia in grasslands, savannah and shrub communities (Figure 7i).

Etymology

Named after Peter Raymond Baverstock, Head, Evolutionary Biology Unit, South Australian Museum, in recognition for his contribution to the understanding of the systematics of Australian mammals.

Specimens examined

Paratypes

New South Wales: Tarawi Stn (33°26′S, 141°07′E) 1 ♀, 1 ♂, EBU (B368, B369).

Northern Territory: Alcoota Stn (22°44′S, 134°24′E) 1 ♂, EBUB290.

Queensland: Babbiloora Stn (25°10′S, 147°19′E) 1 ♀, EBUB339.

South Australia: Nr Oraparrina (31°21′S, 138°37′E) 1 ♀, 2 ♂, EBU (SP105, SP107-8); Danggali Conservation Park (*ca.* 33°30′S, 140°42′E) 1 ♀, 8 ♂, EBU (D1, D2, D7, D10, D12, D17, D27, D23, E66); 25 km N Morgan (34°50′S, 139°42′E) 1 ♀, 1 ♂, EBU (SP62, SP65); North Mulga Stn (30°10′S, 139°40′E) 1 ♀, 1 ♂, EBU (B389, B390); 17 km S Oodnadatta (27°37′S, 135°34′E) 2 ♂, EBU B405-6.

Western Australia: Mt Elvire (29°30′30″S, 119°36′00″E) 1 ♀, WAM18293; White Quartz Dam (29°54′00″S, 121°15′05″E) 1 ♂, WAM17548.

Morphometric analyses: results and discussion

Univariate analyses

The means and standard deviations of the 39 skull and external measurements for the nine species are shown in Table 1.

The ANOVA revealed significant ($P<0.05$) sexual dimorphism in 23 of 39 measurements examined, with females larger in each of the 23 measurements. The 23 measurements consisted of 16 of the skull characters (GL, AOB, LW, ROL, ZW, MW, BW, PL, BL, BB, RC^1-LC^1, M^1-M^3, RM^3-LM^3, LR, DL, RC) and seven external measurements (HV, TV, EL, RL, MCIII, PI, PII).

The species-area combination were highly significant ($P<0.001$) for all characters and six of the 39 characters showed a siginificant ($P<0.05$) interaction between sex and species-area combinations. This indicates that the degree of sexual dimorphism may vary between species and area for the six characters (ZW, BL, BUL, C^1-M^3, M^1-M^3 and DL).

Phenetic analyses

Canonical variate analysis

Canonical variate analysis was used to examine the variation between 18 groups formed by separating the nine species by the sexes (Figure 17). All skull and external measurements were used in this analysis except for zygomatic width and tail length which were missing from many specimens. These two measurements have been omitted from all subsequent analyses. This analysis showed that the differences in group means for males and females were less than differences between species. As a result the sexes were combined for subsequent analyses.

A canonical variate analysis was carried out on the nine species based on skull and external characters. The scatter of the individual samples about the first two

Table 2 Standardised and unstandardised (in brackets) coefficient for the skull and external characters for the first two canonical variates shown in Figure 18a.

CHARACTER	Variate I	Variate II	Variate III
GL	.119 (.351)	−.216 (− .637)	.149 (.441)
AOB	−.544 (−3.195)	−.087 (− .509)	− .156 (− .917)
LOW	.371 (2.595)	.360 (2.517)	− .122 (− .852)
LW	−.155 (− .787)	−.048 (− .243)	.110 (.558)
ROL	.215 (.963)	.008 (.035)	.081 (.365)
MW	.062 (.295)	−.204 (− .972)	.486 (2.312)
BW	.276 (1.412)	−.028 (− .146)	.017 (.088)
CH	−.336 (−2.058)	.594 (3.642)	.016 (.101)
LCH	.245 (1.350)	.028 (.155)	.098 (.539)
PL	.100 (.455)	.318 (1.455)	− .201 (− .917)
BL	.035 (.103)	−.086 (− .256)	.275 (.814)
PPW	.146 (1.220)	.232 (1.933)	− .167 (−1.393)
BUL	.048 (.442)	.053 (.485)	− .080 (− .734)
BB	.257 (1.917)	−.098 (− .730)	.038 (.282)
OB	−.072 (− .396)	−.097 (− .533)	− .099 (− .545)
CW	.013 (.196)	−.263 (−3.926)	.058 (.870)
RC^1-LC^1	−.102 (− .609)	−.232 (−1.379)	.349 (2.075)
C^1-M^3	.277 (1.624)	.088 (.519)	− .190 (−1.117)
M^1-M^3	−.065 (− .512)	.102 (.804)	.511 (4.017)
M^2 L	−.077 (−1.170)	.107 (1.617)	− .147 (−2.217)
M^2 W	.083 (1.110)	−.121 (−1.616)	.093 (1.241)
M^3 W	−.007 (− .085)	.041 (.532)	.025 (.326)
RM^3-LM^3	−.218 (−1.173)	.418 (2.251)	− .249 (−1.341)
LR	.089 (.455)	.302 (1.549)	− .337 (−1.731)
DL	.495 (1.622)	−.698 (−2.287)	.373 (1.224)
RC	−.087 (− .717)	.193 (1.581)	− .426 (−3.492)
HV	.026 (.011)	−.114 (− .047)	− .177 (− .074)
EL	−.075 (− .106)	−.064 (− .091)	.057 (.081)
EW	.176 (.410)	−.155 (− .363)	.286 (.667)
TL	−.021 (− .386)	−.051 (− .092)	− .093 (− .169)
RL	−.332 (− .260)	.519 (.407)	.529 (.415)
MCIII	−.551 (− .442)	−.035 (− .028)	.404 (.323)
PI	.523 (.944)	.468 (.846)	−1.011 (−1.826)
PII	−.829 (−1.332)	−.134 (− .215)	.046 (.073)
PIII	.414 (.713)	.143 (.247)	− .260 (− .447)
TIB	.029 (.045)	−.131 (− .208)	.064 (.102)
PL	.265 (.643)	−.019 (− .047)	.310 (.754)
CONSTANT	−12.344	−25.271	−25.721

mean canonical variates indicates that *E. caurinus*, *E. finlaysoni* and *E. troughtoni* are clearly separated from the other species (Figure 18a). Table 2 shows the characters (PII, MCIII, AOB, PI, DL) which were important in the separation of the first canonical variate. The unbiased estimate of correct classification for the analysis was 91 per cent. The UPGMA cluster analysis of the Mahalanobis matrix arising from this analysis and the Minimum Spanning Tree analysis shows a similar separation to the canonical variate analysis (Figure 19a & b, respectively). These relationships were little altered by inclusion of the coded characters or from the size-free treatment.

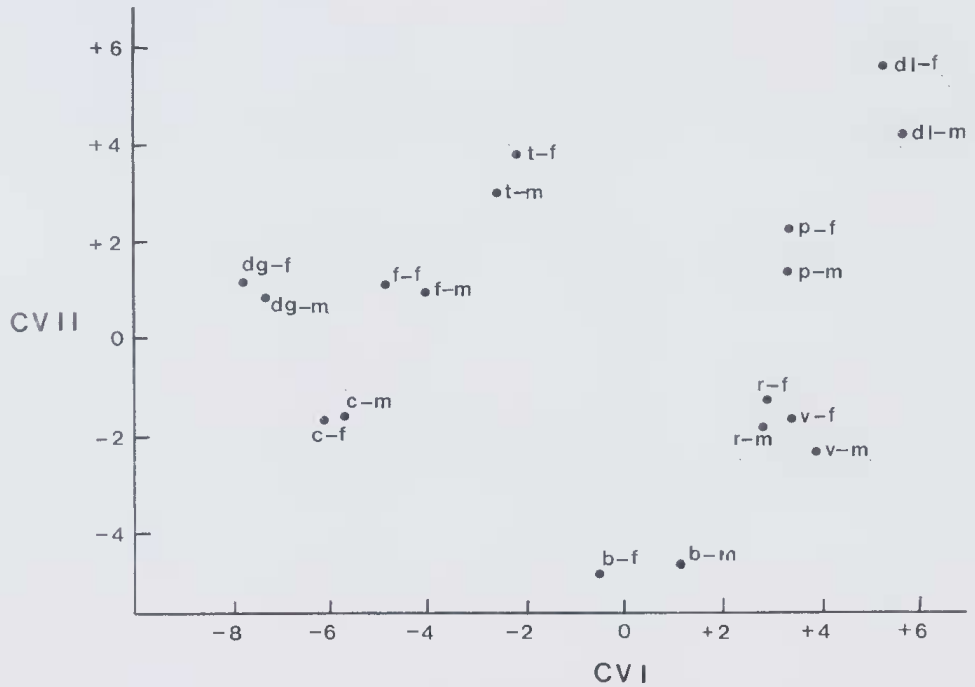


Figure 17 Canonical variate group mean values (●) using the first two variates for males (m) and females (f) of the nine species of *Eptesicus* using skull and external characters. *Eptesicus* species: p, *pumilus;* c, *caurinus;* dg, *douglasorum;* f, *finlaysoni;* dl, *darlingtoni;* t, *troughtoni;* r, *regulus;* v, *vulturnus* and b, *baverstocki.*

The canonical variate analysis on the nine species was repeated for the external characters only and as expected the separation between species is reduced (Figure 18b) compared to the skull and external analysis. Table 3 shows the standardised and unstandardised canonical variate coefficients for this analysis.

To examine the effect of area on these analyses, species with more variable morphology were separated into geographical areas and the canonical variate analysis on the skull and external characters was again undertaken. In general, the mean canonical variates of species from different areas occur close to each other (Figure 20).

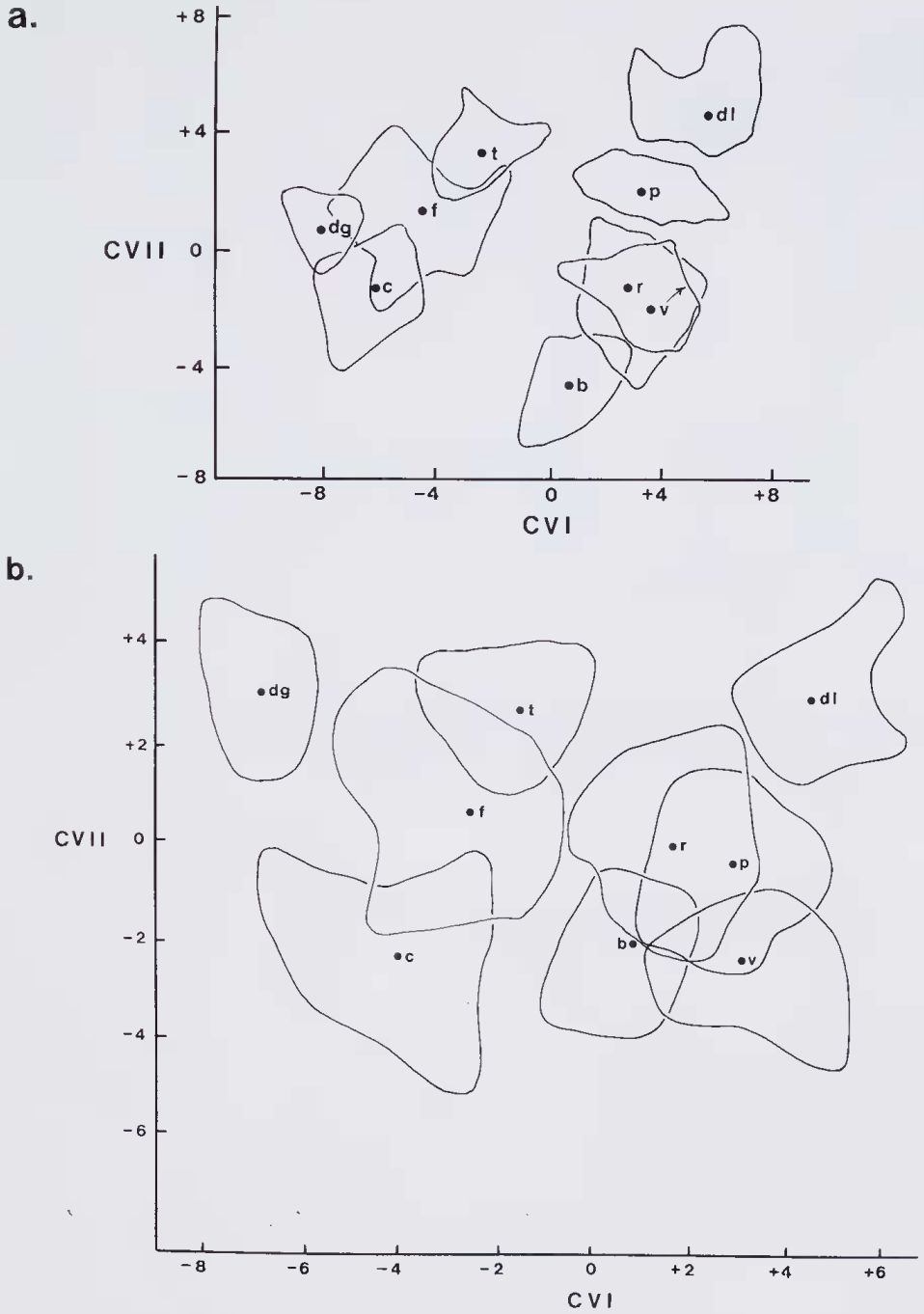


Figure 18 Canonical variate analyses on the nine species of *Eptesicus* (males and females combined) showing the scatter of individual samples about the first two mean canonical variates (●) for (a) skull plus external characters and (b) external characters only.
See Figure 17 caption for species code.

Table 3 Standardised and unstandardised (in brackets) canonical variate coefficients for the external characters for first two variates shown in Figure 18b.

CHARACTER	Variate I	Variate II
HV	.258 (.107)	−.122 (−.050)
EL	− .002 (− .003)	.045 (.063)
EW	.201 (.463)	.117 (.269)
TL	.033 (.060)	−.067 (−.119)
RL	− .187 (− .145)	.701 (.543)
MCIII	− .579 (− .456)	.313 (.247)
PI	.821 (1.466)	.024 (.042)
PII	−1.083 (−1.679)	−.079 (−.122)
PIII	.578 (1.002)	.149 (.258)
TIB	.164 (.253)	−.088 (−.136)
PL	.278 (.686)	.183 (.450)
CONSTANT	−4.202	−26.503

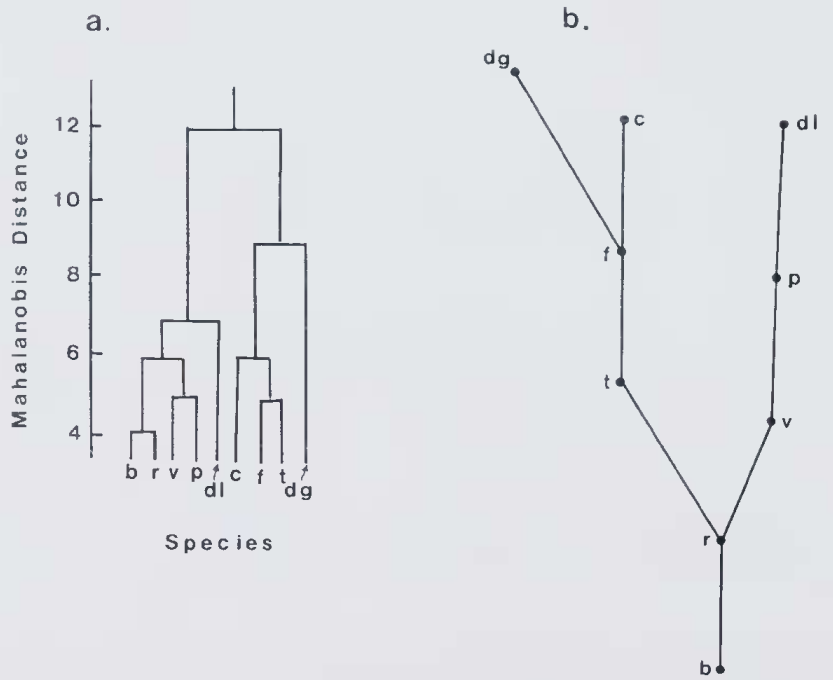


Figure 19 Phenetic relationships of the nine species of *Eptesicus* based on skull and external characters combined for males and females. (a) UPGMA cluster analysis, (b) Minimum Spanning Tree analysis. Species code is as for Figure 17.

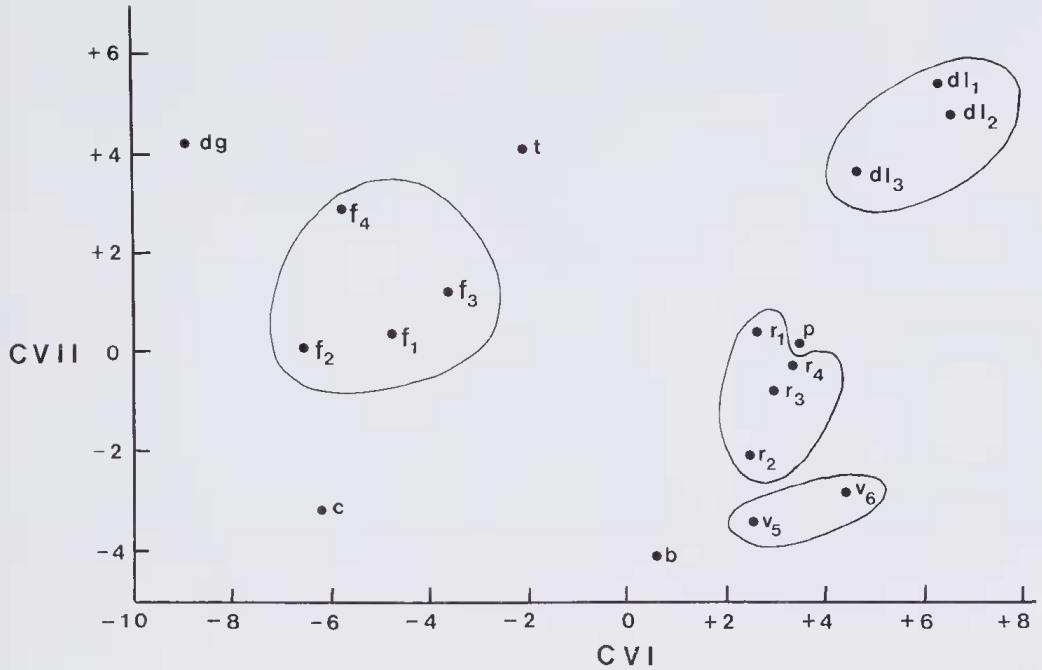


Figure 20 Canonical variate group mean values (●) for the first two variates for males and females of the nine species of *Eptesicus* using skull plus external characters. After first separating the species with the more variable morphology *(finlaysoni, darlingtoni, regulus* and *vulturnus)* into broad geographic groups. See Figure 17 caption for species code. The species numerical subscript denotes the geographic areas which are listed on Figure 7.

To help discriminate the level of difference between *E. caurinus, E. finalysoni* and *E. troughtoni,* a canonical variate analysis of only these species was undertaken with the specimens of the widely distributed and variably sized *E. finlaysoni* separated into its four geographical areas (Figure 7d). This analysis, using the skull and external characters, shows a relatively clear separation of the species (Figure 21). Also, *E. finlaysoni* from area 4 (North West Coastal) is clearly separated from the specimens of *E. finlaysoni* from other areas. The characters which had the highest standardised canonical variate coefficients on the first canonical variate were GL (0.79), AOB (-0.68), LW (0.43), M^2W (-0.41) and RL (-0.40), while the characters with largest coefficients on the second canonical variate were TIB (-0.86), LOW (0.75), PII (-0.72), RL (0.66) and LW (-0.57). The unbiased estimate of correct classification between the three species was 97 per cent confirming the separation evident in Figure 21.

A similar analysis was undertaken for *E. regulus, E. baverstocki* and *E. vulturnus* with the specimens of *E. regulus* and *E. vulturnus* separated by the areas they occurred in. Figure 22 shows a clear separation of the three species using the skull and external characters. The first canonical variate separates *E. vulturnus* from the other two species and has PI (1.76), MCIII (-0.86), LOW (0.83), LR (0.57) and

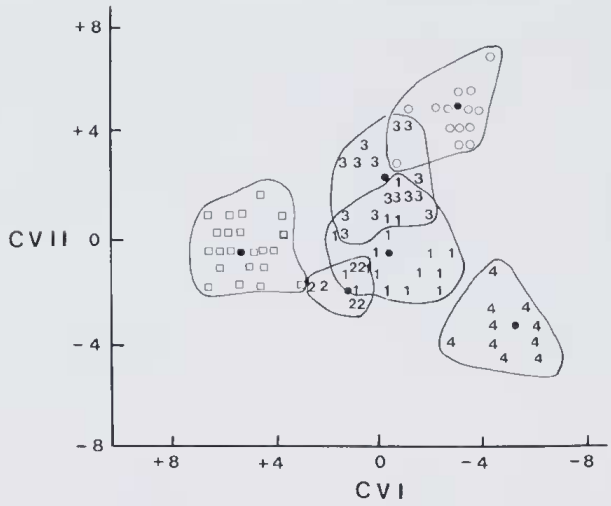


Figure 21 Canonical variate values for the first two variates using skull plus external characters for males and females combined. □, *Eptesicus caurinus;* 1-4, *E. finlaysoni* and ○, *E. troughtoni. E. finlaysoni* geographic groups are 1, Central West; 2, Pilbara; 3, Central East and 4, North West Coastal – see Figure 7d. ●, group means.

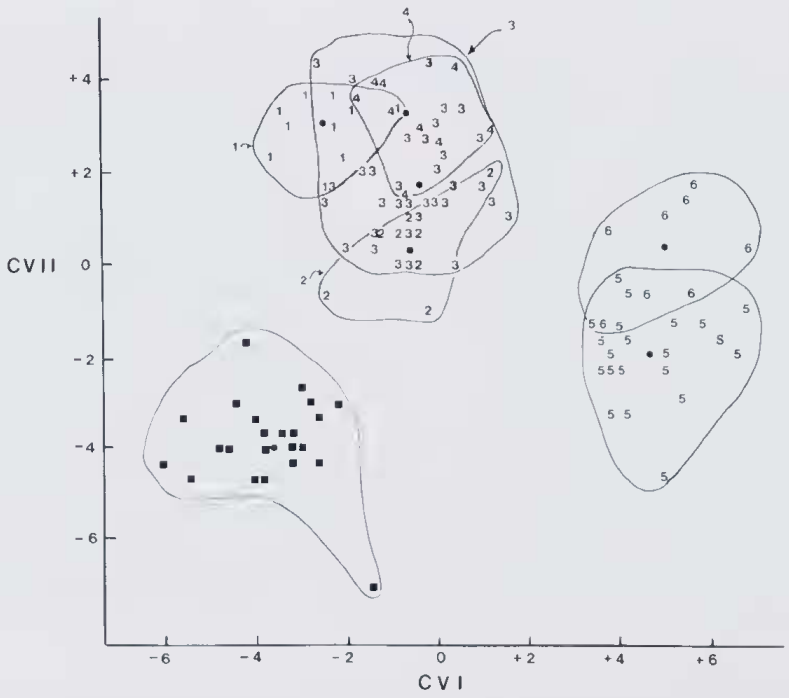


Figure 22 Canonical variate values for the first two variates using skull plus external characters for males and females combined. ■, *E. baverstocki;* 1-4, *E. regulus* and 5-6, *E. vulturnus. E. regulus* and *E. vulturnus* geographic groups are indicated on Figure 7g and h.

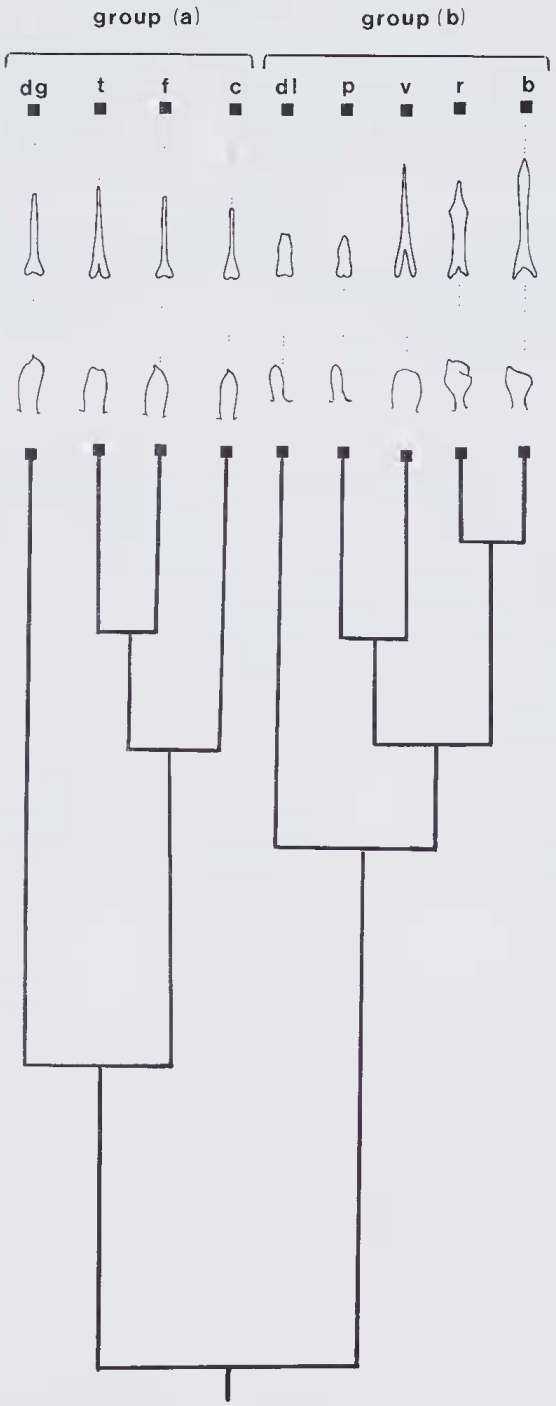


Figure 23 Phenetic relationship (see Figure 19a) of *Eptesicus* species and the outline of their associated baculum (upper row, dorsal view – see Figure 5) and glans penis (lateral view – see Figure 4).

CH (-0.54) with the highest standardised coefficients. The second variate separates *E. regulus* from *E. baverstocki* with LOW (0.64), PII (-0.52), MW (0.50), C^1-M^3 (0.41) and LCH (0.39) having the highest coefficients. The unbiased estimate of correct classification between the three species was 98 per cent.

Discussion

Electrophoretic data are available for all species considered in this revision. These data which generally support the taxonomy proposed herein (M. Adams pers. comm.), will be published separately by our colleagues at the Evolutionary Biology Unit, South Australian Museum.

The taxonomy resulting from this study differs more from McKean *et al.* (1978) (the most recent revisers of *Eptesicus*) than may be immediately apparent. In addition to synonymising *E. sagittula* with *E. darlingtoni,* most, if not all, of the specimens which these authors attribute to *E. pumilus pumilus* are representative of *E. troughtoni.* Their more coastal specimens of *E. pumilus caurinus* represent *E. caurinus* – while the more inland specimens represent *E. finlaysoni.* Our concept of *E. vulturnus* and *E. regulus* is that of McKean *et al.* (1978).

The morphological variation in *E. finlaysoni,* as evidenced by the standard deviation values in Table 1, is much higher for most characters than is the case with other *Eptesicus* species. Grouping of specimens of *E. finlaysoni* into four broad geographic regions (Figure 7d) reduces considerably this variation within each region and attributes much of the overall variation in this species to the large North West Coastal form (see Figure 21). There may be future grounds for recognising this latter form as a distinct taxon but this consideration should not precede more extensive collection in areas intermediate between it and the Pilbara and Central West regions.

Individual *E. caurinus, E. finlaysoni* and *E. troughtoni* may on occasions be difficult to distinguish from each other. In these cases, measurements of skull and external characters enabled their classification with considerable confidence using the canonical variate analysis (Figure 21) – particularly when note is taken of the geographical area of the specimen. Similarly, the occasional difficult to identify specimens of *E. regulus, E. vulturnus* and *E. baverstocki* were correctly classified using the canonical variate analysis in Figure 22.

The phenetic analyses, using UPGMA and Minimum Spanning Tree procedures on continuous external and skull measurements are concordant in the relationships they show for the *Eptesicus* species. The UPGMA analyses more graphically shows the presence of two phenetic groups within *Eptesicus.* These are (a) *caurinus, finlaysoni, troughtoni* and *douglasorum* and (b) *baverstocki, regulus, vulturnus, pumilus* and *darlingtoni.* The integrity of these two phenetic groups are offered independent support by the morphology of the glans penis and baculum of these species (Figure 23). The four *Eptesicus* species in the phenetic group (a) all have a similar glans and baculum (*E. troughtoni* differs most but its glans and baculum

are clearly allied with group (a) rather than the other phenetic group). Within the phenetic group (b) there are three rather distinct glans and baculum types. That of *darlingtoni/pumilus, regulus/baverstocki* and *vulturnus*. The phenetic separation of *E. douglasorum* and *E. darlingtoni* within these two groups probably reflects their relative large size compared to the other species, although a 'size free' analysis did not alter these overall relationships.

These two *Eptesicus* phenetic groups relate to broad distribution patterns of the species. Those species with a northern distribution are members of the phenetic group (a) and those with a southern distribution are in group (b). Species with a wide inland distribution are in both groups (a) and (b).

Key to Australian ***Eptesicus*** species (measurements in mm)

1 Manus digit III with phalanx III: phalanx II length >0.75; distance between anteorbital foramina: rostrum length <0.78; anterior narial emargination deep or broad; basolateral pterygoid wing present or absent; baculum curved distally or flat in lateral profile; glans penis dorsoventrally compressed or not compressed 2

Manus digit III with phalanx III: phalanx II length <0.75; distance between anteorbital foramina: rostrum length >0.78; anterior narial emargination narrow parabolic shape; basolateral pterygoid wing present; baculum bow shaped in lateral profile; glans penis laterally compressed 6

2 Manus digit III with phalanx III: phalanx II length generally >0.84; anterior narial emargination V-shaped; basolateral pterygoid wing present, partially conceals foramen rotundum; cranial height: basicranial length >0.42; baculum length <2 mm; glans penis dorsoventrally compressed 3

Manus digit III with phalanx III: phalanx II length generally <0.84; anterior narial emargination broader, oval; basolateral pterygoid wing absent; cranial height: basicranial length <0.42; baculum length >3 mm; glans penis not dorsoventrally compressed 4

3 Radius length averages 34.6 (32.5-37.2); manus digit III with phalanx III: phalanx II length average 0.92; greatest skull length averages 13.4 (12.7-14.1); anterior narial emargination extends to (or almost to) a line joining anteorbital foramina; dorsal inflation of cranium slight to moderate; baculum distal end square ..... *E. darlingtoni*

Radius length averages 30.6 (28.1-32.9); manus digit III with phalanx III: phalanx II length average 0.87; greatest skull length averages 12.1 (11.3-12.7); anterior narial emargination shallower, rarely extends to line joining anteorbital foramina; dorsal inflation of cranium pronounced; baculum distal end pointed ..... *E. pumilus*

4 Manus digit III with phalanx I: metacarpal length >0.40 (averages 0.42); glans penis bulbous; baculum base notched to *ca.* 25 per cent its length. ..... *E. vulturnus*

Manus digit III with phalanx I: metacarpal length <0.40; glans penis not bulbous; baculum base notched <20 per cent its length 5

5 Posterior margin of palate terminates level with or slightly posterior to anterior edge of sphenorbital sinus. General size larger – greatest skull length averages 12.7 (11.9-13.4), radius length 31.2 (28.0-34.4); glans penis with large lateral urethral folds; baculum dart shaped ..... *E. regulus*

Posterior margin of palate terminates well posterior to the anterior edge of sphenorbital sinus; general size smaller – greatest skull length averages edge of (11.6-12.5), radius length 28.8 (26.7-31.4); glans penis funnel shaped, without lateral urethral folds; baculum narrow with broad base..... *E. baverstocki*

6. Radius length averages 29.5 (26.6-31.7);M^1 metacone-hypocone crista moderate or large; greatest skull length averages 11.2 (10.6-12.0); cranial height: basicranial length averages 0.47. Distribution does not include Pilbara region ..... *E. caurinus*

Radius length averages 34.6 (29.8-37.6) – only Pilbara *E. finlaysoni* <31.7; M^1 metacone-hypocone crista absent or slight to large 7

7 Manus digit III with phalanx I: metacarpal length <0.34 (averages 0.32); M^1 metacone-hypocone crista moderate; radius length averages 36.2 (34.3-37.6) ..... *E. douglasorum*

Manus digit III with phalanx I: metacarpal >0.34 (averages 0.37); M^1 metacone-hypocone crista usually absent, rarely slight to moderate 8

8 Radius shorter relative to tibia (Figure 10); glans penis distally pointed; baculum base notched to <10 per cent its length; M^1 metacone-hypocone crista always absent..... *E. finlaysoni*

Radius longer relative to tibia (Figure 10); glans penis not pointed; baculum base notched to *ca.* 25 per cent its length; M^1 metacone-hypocone crista absent to moderate ..... *E. troughtoni*

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Appendix

Measurement (in mm) of relevant type specimens examined. See Figure 1 for description of characters. Preservation code: SS – skull and dry skull; SA – dry skull and body in alcohol.

Species Catalogue No., Type, Sex, Preservation	***Eptesicus pumilus***, BMNH 41.1523 (119c) lectotype, A ♂, SS	***Eptesicus caurinus***, BMNH 14.3.9.1.10473, holotype, A ♂, SA	***Eptesicus douglasorum***, WAM M3405C, holotype A ♂, SA	***Eptesicus finlaysoni***, WAM M22407, holotype A ♂, SA	***Eptesicus darlingtoni***, J5476, paratype, A ♀, SS	***Eptesicus sagittula***, CM2290, paratype, A ♂, SS	***Eptesicus troughtoni***, JM 5412, holotype A ♂, SA	***Eptesicus regulus***, BMNH 6.8.1.18, lectotype A ? sex, skull only	***Eptesicus vulturnus***, BMNH 7.1.1.375, holotype, A ♀, SS	***Eptesicus baverstocki***, WAM M17812, holotype, A ♂, SA
GL	–	11.1	12.6	11.4	13.2	13.2	12.8	12.5	12.5	12.2
AOB	*3.9-4.2	3.8	4.3	3.9	4.2	4.1	4.4	3.9	4.0	3.7
LOW	3.5	3.1	3.4	3.3	3.8	1.1	3.6	3.4	3.6	3.2
LW	4.5	4.3	5.5	4.9	5.5	5.3	5.6	4.6	4.8	4.8
ROL	5.0	4.3	5.2	4.9	5.3	5.7	5.4	5.0	5.2	5.2
ZW	–	7.1	8.4	7.5	–	8.3	8.2	7.8	8.2	7.8
MW	–	6.3	–	6.7	7.8	7.6	7.4	7.2	7.4	6.9
BW	–	5.8	6.1	5.7	6.6	6.7	6.3	6.4	6.8	6.2
CH	–	4.4	4.9	4.5	4.8	5.0	4.8	4.7	4.2	4.4
LCH	–	1.5	2.2	1.8	2.2	2.2	2.3	2.1	2.4	2.0
PL	–	5.0	5.9	5.2	6.0	5.9	6.1	5.6	5.8	5.5
BL	–	9.3	10.7	9.8	11.0	11.2	10.9	10.7	10.5	10.4
PPW	–	1.4	1.5	1.6	1.8	1.9	1.6	1.5	1.7	1.4
BUL	–	2.7	2.7	2.6	3.0	3.1	2.9	–	2.8	2.7
BB	–	1.0	1.1	0.9	1.3	1.1	1.2	1.2	1.3	1.1
OB	–	5.8	6.4	–	7.3	7.0	6.5	6.5	6.7	6.3
CW	0.9	0.8	0.8	0.7	0.7	0.7	0.8	1.0	0.9	0.7
RC^1-LC^1	3.7	3.4	3.9	3.7	4.0	3.9	4.3	3.7	3.8	3.7
C^1-M^1	4.3	3.9	4.6	4.4	4.8	4.9	4.6	4.7	4.6	4.2
M^1-M^1	2.8	2.7	3.1	2.8	3.2	3.3	3.1	3.2	3.1	2.9
M^2L	1.1	1.1	1.2	1.0	1.3	1.3	1.1	1.4	1.2	1.1
M^2W	1.2	1.2	1.3	1.2	1.4	1.4	1.4	1.4	1.4	1.2
M^3W	1.3	1.2	1.2	1.2	1.3	1.4	1.3	1.4	1.4	1.2
RM^3-LM^1	5.0	4.7	5.3	5.2	5.6	5.5	5.5	4.3	5.4	4.9
LR	5.4	4.9	5.6	5.0	5.9	5.9	5.8	5.8	5.8	5.0
DL	8.5	8.0	9.1	8.0	9.1	9.7	9.3	8.9	9.0	8.2
RC	2.5	2.4	2.8	2.3	2.6	2.7	2.6	2.5	2.7	2.3
HV	–	36.5	39.6	36.0	–	–	41.6	–	–	37.5
TV	–	24.4	37.1	33.6	–	–	32.9	–	–	27.4
EL	–	9.5	11.6	11.6	–	–	12.4	–	–	9.8
EW	–	6.5	8.4	7.8	–	–	8.2	–	–	8.7
TL	–	4.4	6.1	4.9	–	–	6.2	–	–	4.6
RL	29.7	29.5	36.4	31.3	36.3	33.7	35.1	–	32.8	27.3
MCHH	30.3	27.6	36.3	30.6	34.5	33.6	34.6	–	31.1	27.6
PI	10.9	10.4	11.4	11.3	13.5	12.1	13.2	–	10.7	10.2
PII	9.1	10.0	11.9	9.5	10.3	9.7	11.2	–	8.2	9.3
PIII	–	5.9	6.5	6.7	–	–	7.8	–	6.0	6.6
TTB	12.8	11.2	14.1	12.9	–	–	14.2	–	12.6	11.3
PL	5.2	4.3	6.1	4.1	–	–	5.7	–	–	4.7

* 2 small left anteorbital foramina

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